CHARLES UNIVERSITY IN PRAGUE
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MASTER THESIS

Palaeodictyoptera: morphology of immature wings from the Upper Carboniferous of Poland

Morfologie křídelní nervatury larválních stádií Palaeodictyoptera ze svrchního karbonu Polska

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Declaration:

I declare this thesis is a result of my own work, except for the contribution of people stated in acknowledgements. I properly cite all information sources used. This thesis or its part was submitted to obtain neither another nor same academic degree.

Prohlášení:

Prohlašuji, že jsem závěrečnou práci vypracovala samostatně, a že jsem uvedla veškeré použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

In Prague, 15th August, 2013

ABSTRAKT

Hmyzí křídla představují vysoce specifické a unikátní struktury v celé živočišné říši. Morfologie hmyzího křídla je výsledkem dlouhotrvajících složitých evolučních procesů, a doposud není zcela vyjasněno, jakým způsobem se hmyzí křídla vyvíjela, ačkoli schopnost létat je jednou z nejvýznamnějších událostí v evoluci hmyzu, jelikož umožnila osídlit nová prostředí, efektivně uniknout před predátory, nebo najít partnera ke spáření.

V této diplomové práci představujeme nově objevený unikátní materiál juvenilních stádií Palaeodictyoptera ze svrchního karbonu (westfal A) Polska. Tento řád vyhynul na konci permu, nicméně v průběhu pozdního Paleozoika byl pozoruhodně diverzifikovaný. Doposud bylo popsáno několik dospělců z tohoto řádu, nicméně znalosti týkající se nedospělých stádií jsou poměrně skrovné z důvodu nedostatečného množství vhodných fosilních specimenů. Imaturní křídla popsaná v této diplomové práci beze sporu patří do řádu Palaeodictyoptera, a byla přiřazena k nadčeledím Breyeroidea a Homoiopteroidea. Nicméně jejich zařazení k čeledím Breyeriidae (morphotype A) a Homoiopteridae (morphotype B) založené na znacích křídelní žilnatiny na předních křídlech není jednoznačné vzhledem k pouze částečně vyvinuté žilnatině u juvenilních stádií.

Cílem této diplomové práce je komplexně popsat 14 nových imaturních křídel, upozornit na důležité morfologické struktury, které se u nedospělých křídel vyskytují (např. přítomnost žilky CP oddělené od anteriorního okraje křídla nebo výrazný kýl na předním křídle) a revidovat znalosti týkající se vývoje křídla.

klíčová slova: Insecta, Palaeoptera, Palaeodictyoptera, křídelní žilnatina, morfologie a vývoj křídla, taxonomie, nymfa, svrchní karbon, Polsko

ABSTRACT

Insect wings are very specific and unique structures in animal kingdom. Wing morphology is a result of long-standing complicated evolutionary process and until recently the way how the wings have evolved is not completely clarified. The flight ability is one of the most important event in insect history because it allows them to exploit new habitats, escape from predators or find the sexual partner.

Here we present the newly discovered material consisting of Palaeodictyoptera immature wings from the Upper Carboniferous (Westphalian A) of Poland. This order became extinct in the end of Permian, however during the Late Paleozoic was remarkably diversified. Until recently, number of adult palaeodictyopterans have been described, however the immature stages are relatively unknown due to lack of suitable fossils. Immature wings present in this thesis have undoubtedly palaeodictyopterous affinities with atribution within superfamilies Breyeroidea and Homoiopteroidea. However, their familial assignment into Breyeriidae (morphotype A) and Homiopteridae (morphotype B) based on fore wing venation characters is not definite because of wing venation limits in early ontogenetic stages.

The aim of the present work is a complex description of 14 new palaeodictyopteriids immature wings, and to point out certain important morphological structures (e.g., the presence of CP separated from anterior margin of the wing as proposed by Kukalová-Peck (1978), prominent keel in forewings) as well as review of our knowledge about immature wing development.

keywords: Insecta, Palaeoptera, Palaeodictyoptera, wing venation, wing development and morphology, taxonomy, nymph, Upper Carboniferous, Poland

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1. INTRODUCTION

1.1 Arthropod phylogeny with reference to Insects

Insects represent the most succesful macroscopic group of organisms in terms of taxonomic diversity. Approximately 80 % of all described animal species belong to Hexapoda (Insecta *s.l.*), which is the largest group of the phylum Arthropoda (Labandeira, 1999; Bradley et al., 2009).

Manton (1977) have proposed that Hexapoda are the sister group of Myriapoda, together forming Atelocerata (Tracheata). Features defining taxon Atelocerata were as follows: the loss of the second pair of antennae, the presence of tentorium, respiratory system consisting of tracheal tubules, and the presence of Malphigian tubules. Based on the assumption that Atelocerata represents a natural group, several concepts regarding the phylogeny of Arthropoda have been established, but each of these concepts was later rejected (Giribet et al., 2001)

Recently, studies based on molecular data agree that Arthropoda are monophyletic (Turbeville, 1991; Wheeler et al., 1993) and close relationships of crustaceans and hexapods are suggested by molecular studies (Trautwein et al., 2012). Crustacea and Hexapoda form the monophyletic taxon Pancrustacea (Giribet et al., 2001; Kjer, 2004; Meusemann et al., 2010) and this finding is of exceptional importance, because it is inconsistent with previously traditionally accepted concept of Atelocerata (Averof & Cohen, 1997; Kristensen, 1991; Grimaldi & Engel, 2005; Kjer, 2004; Nardi et al., 2003; Regier et al., 2008).

The assumption, that Hexapoda are rather allied to Crustacea has gained considerable support from mitochondrial genes (Boore et al., 1998; Giribet et al., 2001). According to the other authors, Hexapoda are even highly modified Crustacea (Nardi et al., 2003). Relationships between Hexapoda and Crustacea are also supported by several morphological characters - the brain´s structure, the composition of ommatidia or structure of hypopharynx (Klass, 2009; Bradley et al., 2009).

According to this new view, characters shared by Myriapoda and Hexapoda (e.g. tracheal system, Malphigian tubules, or completely fused second maxillae) have evolved independently in two separate lineages (Kukalová-Peck, 1991; Trautwein, 2012).

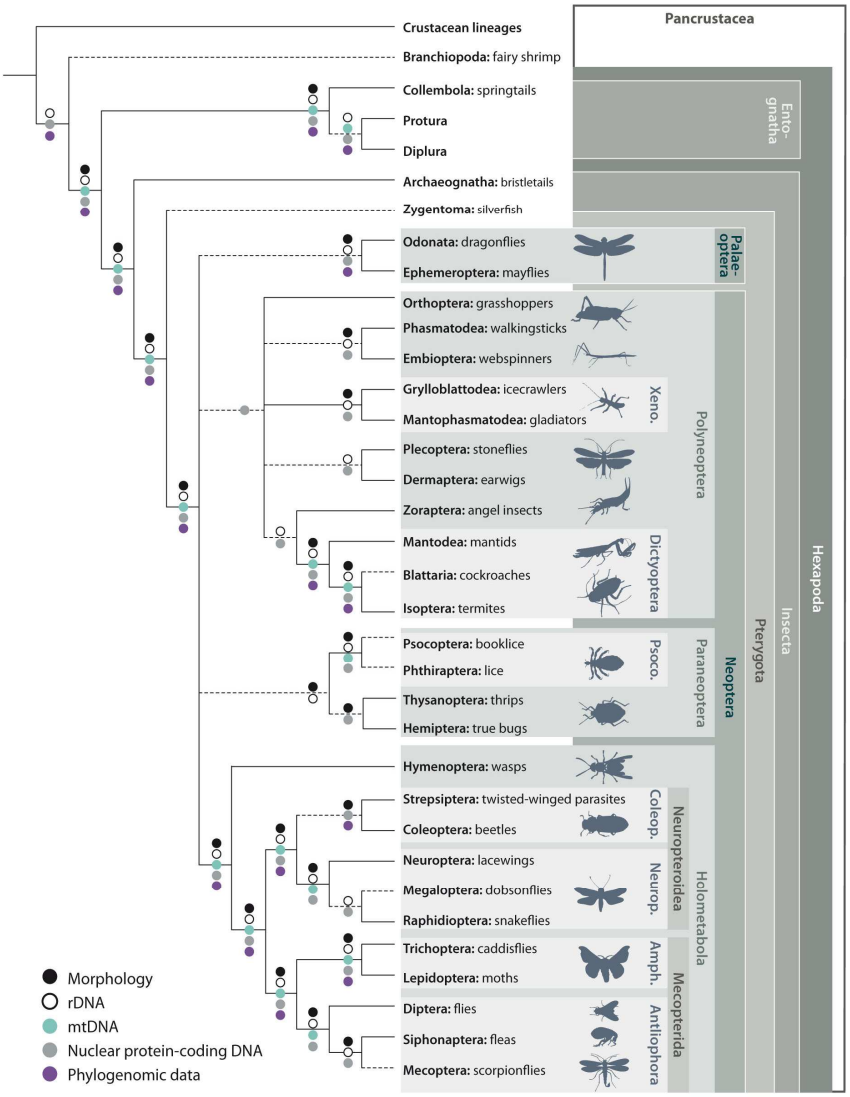


Figure 1. Tree represents the best current estimate of insect relationship based on a review of recent literature. Dashed lines indicate tenuously supported relationships or possible nonmonophyly (in the case of terminal branches). The types of data supporting each node are displayed if a node was recovered by a particular line of evidence alone or in a combined analysis. Phylogenomic data refer to a molecular data set of at least 20 kb, to data collected through EST harvest, or to large-scale genome comparison. Abbreviations: EST, expressed sequence tag; mtDNA, mitochondrial DNA; rDNA, ribosomal DNA; Amph., Amhiesmenoptera; Coleop., Coleopterida; Neurop., Neuropterida; Psoco., Psocodea; Xeno, Xenonomia (Trautwein et al., 2012).

Monophyly of Pancrustacea clade is well supported, but it is still very important to resolve which of the crustacean lineages is the closest relatives to Hexapoda. Results from multigene and phylogenomic analyses show that the closest relatives of Hexapoda are Branchiopoda (Aleshin et al., 2009; Meusemann et al., 2010; Regier et al., 2008), while results from another phylogenomic studies suggest that obscure groups Remipedia and Cephalocarida are the sister groups of Hexapoda (Regier et al., 2010), and studies based on morphological traits consider the group Remipedia as the sister group of Hexapoda (Ertas et al., 2009).

Most of recent concepts regarding on Hexapoda phylogeny is based on the fundamental works of Hennig (1969, 1981), Boudreaux (1979), and Kristensen (1991). According to Kristensen (1991), the Hexapoda can be divided into the Collembola, Protura, Diplura, and Insecta (Ectognatha). Collembola, Diplura and Protura, together forming Endognatha, are primarily wingless insect orders (Trautwein, 2012).

For a long time, Hexapoda have been regarded as monophyletic, because of all members shared unique tagmosis pattern (head, thorax, abdomen), and three pairs of thoracic limbs (Hennig, 1969; Kristensen, 1991; Regier et al., 2004). Relationships between entognathans and insects have been challenged because of comparison of mitochondrial genomes found that collembolans are more closely related to Crustacea (Nardi et al., 2003; Carapelli et al., 2007). Nardi et al. (2003) have analyzed 1305 aminoacids from mitochondrial cytochorome oxidase complex, and analysis have shown that most insects were related to Crustacea and Collembola was the sister group of Crustacea and Insecta. Nevertheless, their results have been critisized by Delsuc et al. (2003) who argued that in nucleotides there are more informations regarding the insect phylogeny than in aminoacids. They made their own analysis based on nucleotide data, and their results supported the monophyly of Hexapoda. Other rDNA analyses recovering monophyly of Hexapoda were made by Giribet et al. (2004) or Luan et al. (2005).

Within Insecta, there are two primarily wingless insect orders Archaeognatha and Zygentoma. Members of these two orders are similar and thus they were previously grouped in Thysanura, forming the sister group of winged insects

(Grimaldi & Engel, 2005). Members of order Zygentoma were found to be closer relatives to winged insects, forming the group Dicondylia characterized by mandibles with two point of articulation (Regier et al., 2010; Wheeler et al., 2001). Therefore, in Insecta a basal split is proposed between Archaeognatha and Dicondylia (Klass, 2009).

Currently, the monophyly of Hexapoda is resolved, but clarification of the relationships of early-diverging lineages of winged insects still remains problem, despite the application of both phylogenomic and morphological data.

Martynov (1923) was the first who established a basal division of all winged insects into two main groups, Palaeoptera and Neoptera, on the basis of wing articulation.

Palaeoptera is recently represented by only two insect orders Ephemeroptera and Odonata, although during the Paleozoic era palaeopteran were much more diversified and included extinct orders Diaphanopterodea, Megasecoptera, Palaeodictyoptera and Permothemistida (Kukalová-Peck, 1991; Carpenter, 1992). Division into Palaeoptera and Neoptera was later challenged, because there were several apomorphic characters shared by dragonflies and neopterans, e.g. the number and position of the articulations of the mandibles, subimago stage, or annulated caudal filament, thus some authors supposed that Ephemeroptera represents basal clade, and Odonata and Neoptera are the sister groups (Kristensen, 1991). Also the comparison of mitochondrial genomes and some morphological studies have recovered order Odonata as the closest relatives to Neoptera, together forming group Metapterygota (Cameron et al., 2009; Zhang et al., 2008). On the other hand, according to Willkomen & Hörnschemeyer (2007) Odonata represent basal clade, because of flight muscles and longitudinal veins shared by mayflies and neopterans and because of their similar wing base. Also according to Simon et al. (2009), Neoptera and Odonata are the sister groups together forming Chiastomyaria.

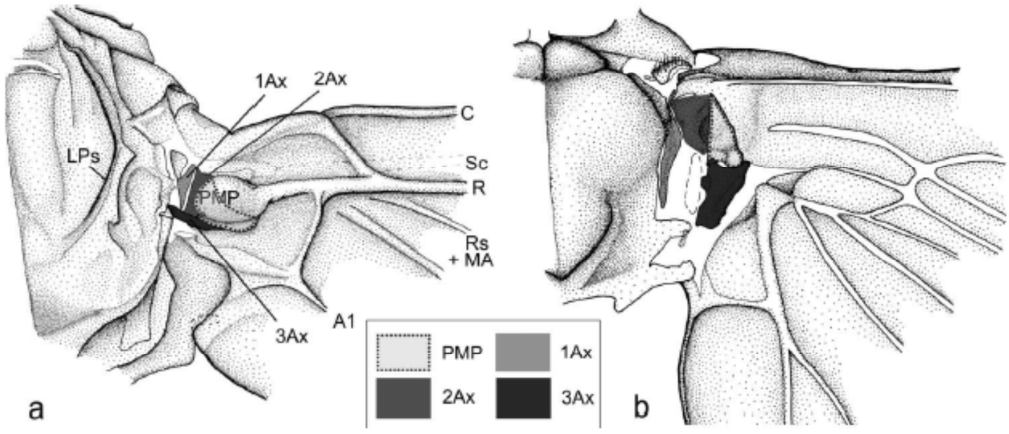


Figure 2. Homology of the axillary sclerites of Ephemeroptera and Neoptera (modified after Willkommen 2008). (a) *Habroleptoides confusa* (Ephemeroptera), right forewing. (b) *Perlodes microcephalus* (Plecoptera), right hind wing (Willkommen, 2009)

The branching of the basal lineages of winged insects has proved a problem for biologists since it was first investigated in the early 20th century. Even an application of large phylogenomic data sets has produced support for all three branching patterns.

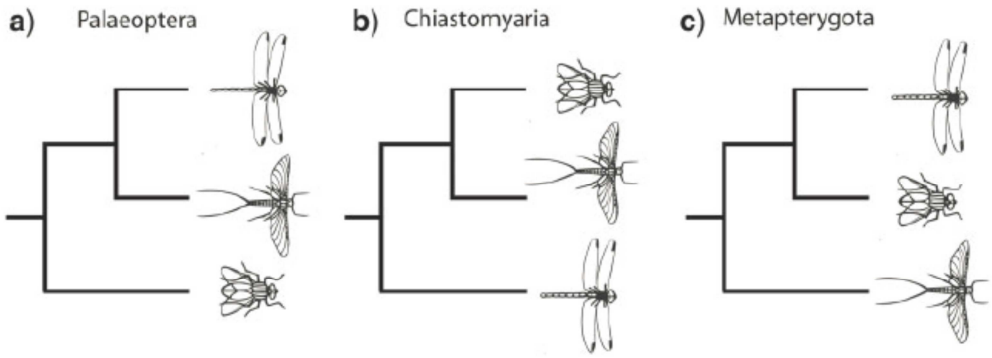


Figure 3. The three hypothesized divisions within the Pterygota (Thomas et al., 2012)

Morphological characters that support monophyly of Palaeoptera are the inability to fold the wings over the abdomen, and the similar wing base in Ephemeroptera and Odonata (Hennig, 1969; Kukalová-Peck, 1991; Kukalová-Peck, 2008). Also recent results from combined analysis of nine genes and 170 morphological characters support the Palaeoptera hypothesis (Kjer et al., 2006). It is also notable

that the support for Palaeoptera is in agreement with those previous studies that used large data sets of many nuclear loci and used the most closely related wingless orders as outgroup taxa (Meusemann et al., 2010; Regier et al., 2010). Over the years, various studies have repeatedly verified the reality of Palaeoptera, and have shown that Odonatoptera is sister group of Ephemeroptera (Kukalová-Peck, 1978, 1983, 1985, 1991; Shear & Kukalová-Peck, 1990).

1.2 Insect development

Generaly, postembryonic development in Hexapoda is epimorphic, which means that juveniles hatching from their eggs have complete number of body segments. The order Protura represents the exception because its development is anamorphic, thus some abdominal segments gradually grow during the postembryonic development (Sehnal et al., 1996).

The earliest forms of insects have shown the direct type of development; they were considered as ametabolous (Truman & Riddiford, 1999). Insects exhibiting this type of postembryonic development belong to the orders Archaeognatha and Zygentoma (Henson, 1946). These insects did not possess the wings, and their earliest stage strikingly resembles the adults except for the absence of external genitalia. During their postembryonic development obvious external changes do not take place. Ametabolous insects develop by a gradual increase in size and they continue to molt even as adults (Sehnal et al., 1996).

Ametabolous type of development was described by Sharov (1953) in *Lepisma saccharina* Linnaeus 1758 (order Zygentoma). Considerable part of the processes of morphogenesis takes place in the egg and thus nymph differs only a little from the imago. The first larval instar has already evolved the homonomous segmentation, although the chaetae are pale and the antennae and caudal setae lack the complete number of segments (Rasnitsyn, 1965).

Molting cycle of each female with ametabolous type of development is preceeded by a yolk deposition and ovulation cycle (Watson, 1964). Molting and ovulation alternates in a mutually exclusive pattern for the remainder of life of the female. This alternation is under neuroendocrine control (Kunkel, 1981).

During the insect development, the juvenile hormone is very essencial. In ametabolous insects, juvenile hormone represses the morphogenesis (Truman & Riddiford, 2002).

Insects with incomplete metamorphosis are termed as Hemimetabola. Hemimetabolous insects contain evolutionary lines Palaeoptera, Polyneoptera and Paraneoptera (see fig. 1; Trautwein et al., 2012).

In hemimetabolous type of development there are several larval instars resembling the adults. Insects with hemimetabolous type of development maintain approximately the same body strucutres during the whole life and therefore the immature stages and adults usually live in the same habitats and utilize the same food sources. In this case, the exception represents the order Ephemeroptera and Odonata. Although these two insect orders are hemimetabolous, they have evolved considerably different nymphal and adult stages thus they can exploit different habitats (Truman & Riddiford, 2002).

In hemimetabolous type of development, the immature stages lacks functional genitalia and they possessed the wing pads on the dorsum of the second and the third thoracic segment. These wing pads evolve gradually into the functional articulated wings throughout molting (Truman & Riddiford, 1999).

Unlike the ametabolous insects in which even adult stages molt, insects with hemimetabolous type of development terminate the process of molting at the moment they reach winged adult stage. The only exception represents mayflies because they molt even after becoming fully winged, in the subimaginal stage (Edmunds & McCafferty, 1988).

Also in hemimetabolan insects, the ontogenesis is leading by juvenile hormone which represses the metamorphosis until the nymph attains an appropriate level of the development. Very little is known about juvenile hormone signaling in insects with hemimetabolous type of development (Konopová et al., 2011).

Some authors suggest that in hemimetabolous insects there are several larval instars and one immature stage which is extremely different, termed as pronymph. The pronymph has some characteristics that make it unique and its morphology is very specific (Truman & Riddiford, 2002). Body proportion of the pronymph are different from those of nymph, the limbs are bent at parts which are not corresponding with joints, cuticle has characteristic ultrastructure and lacks sclerites, mandibles are unsclerotized and there are no wing pads on the dorsum of

the second and the third thoracic segment (Truman & Riddiford, 1999). This stage of insect ontogeny is usually overlooked, but according to Truman & Riddiford (2002) it is possible that pronymph is a basis for the evolution of holometabolous larva.

As it was already mentioned, the vast majority of insects were hemimetabolous during the Carboniferous (Gaunt & Miles, 2002, Garwood et al., 2012). Although some authors suggested that insect with complete metamorphosis were first seen in Permian (Truman & Riddiford, 1999), it was generally assumed that holometabolous insects have appeared at first in the Carboniferous, but until recently there was no convincing evidence for this statement. Not long ago, approximately 310 millions years the oldest fossil of Endopterygota was found in Early Langsettian (Bashkirian), and its finding undoubtely confirmed this statement (Nel et al., 2007).

Holometabola form the monophyletic group, originating from hemimetabolous ancestors during the Permian 300 Mya (Kristensen, 1999), which have evolved a wide range of life-histories (Truman & Riddiford, 2002). Currently the group Holometabola is the most succesful group of terrestrial organisms (Whiting, 2003).

Holometabolous insects have three distinctive ontogenetic stages in its development; larval stage, pupa and adult (Truman & Riddiford, 1999). Because of these developmental stages are obviously different, the juveniles can utilize other habitats and food resources than do the adults one (Nel et al., 2007).

The example of how diversified is the group of holometabolous insects may be different types of mouthparts which is one of the most significant life-history characters in insects. The largest hemimetabolous order Hemiptera contains two different types of mouthparts while each of the four biggest holometabolous orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera) contains approximately from five to six types of mouthparts. Greater diversity at Holometabola can be attributed to the fact that feeding strategies usually differ between juveniles and adults (Yang, 2001).

In holometabolous insects, larval instars possess no external rudiments of wings and genitalia. Imaginal structures evolve from imaginal discs consisting of invaginated clusters of undifferentiated embryonic cells. The wings are invaginated beneath the thoracic cuticle and they do not develop externally. After series of molts and ecdyses, the insects pass into the pupal stage, in which the wing pads are evaginated and become external. The pupal stage is innovation in the holometabolous type of development and it is usually nonfeeding and has limited or supressed locomotory activity. This allows the degradation and rebuilding of the original tissue taking place between the last larval instar and adult stage. This stage already possesses rudimental wings and genitalia (Sehnal et al., 1996).

Some authors suggest that the pupa is the result of the reduction of the nymphal stage of the insects with incomplete metamorphosis to a single instar between the stage of pronymph and the adult stage (Truman & Riddiford, 2002). Another view is that the pupal stage reduced the life span of immatures which are therefore less exposed to predation (Grimaldi & Engel, 2005) and the other authors suggest that the pupa was primarily designed to ensure survival of the insect over periods of seasonal changes. This is not very likely because it is assumed that climate during the early Upper Carboniferous have been warm and humid with dry seasons and the most basal Holometabola had free legs and they were poorly sclerotized (Nel et al., 2007).

In contrast to hemimetabolous insects, neuroblasts at Holometabola begin to proliferate at the certain level of embryogenesis however they produce only an initial set of neurons and then become quiescent. The neuroblasts are reactivating throughout the larval stage generating the remaining neurons which are essential for proper function of nervous system of adult (Truman & Riddiford, 2002).

Because it seems logical that larval stages have evolved earliest than adult ones, it is assumed that nymphs of holometabolous insects are reccuring structures which have already existed in the past. The body plan in insects is formed at the beginning of the development when the blastoderm is forming. After the formation of blastoderm, the embryo begins to differentiate under the influence of

the Hox genes. In holometabolous insects there are established two separate developmental pathways during forming the blastoderm. One of them will give rise to the larval stages and the other one leads to the setting-aside of the imaginal cells that will later form the adult throughout metamorphosis (De Roos, 2006).

The most widely accepted Hinton's model (1976) suppose that the pupal stage at holometabolous insects is essentially a radicalized last instar of hemimetabolous juvenile and therefore that the juvenile and adult stages of the Hemimetabola and Holometabola are homologous. This model was contradicted by Truman & Riddiford (1999), because they realized some neuroendocrinologic and morphologic analyses which have showed them that juvenile stages in Holometabola are in fact homologous with usually overlooked ontogenetic stage called pronymph, which occur in Hemimetabola, as it was mentioned above (Yang, 2001). Berlese (1910) proposed the hypothesis that the complete metamorphosis have evolved by repetition of an embryonic instar and this hypothesis was ressurected by Truman & Riddiford (1999) and followed by Jockusch & Ober (2004).

The taxonomic succes of the insects is largely owed to members of the Homoletabola containing 80-90 % of all extant species. Huge radiation and higher diversity of the group Holometabola over the Hemimetabola has often been attributed to complete metamorphosis allowing divergent evolution in juveniles and adults (Kukalová-Peck, 1991).

1.3 Insect wings

Basal lineages of insects were wingless. The wings have developed in insect evolution, and the development of the wings must be regarded as the most significant event in the evolution of insects. They have gained the flight ability 170, 250, and 350 million years before pterosaurs, birds and bats (Grimaldi & Engel, 2005). The first fossil winged insect *Rhyniognatha hirsti* Tillyard, 1928 is known from Early Devonian of Rhynie, Scotland (Engel et al., 2013).

The winged insect is assumed to be descended from the wingless insects. The first insects possessing the wings, or pro-wings, were probably not able to fly. These pro-wings were present on all thoracic and abdominal segments and the thoracic winglets were primitively functional and later immobilized (Kukalová-Peck, 1978).

Wings have arisen only once in insects, but they have been repeatedly lost (Engel et al., 2013). The development of the wings was gradual and there have been proposed numerous theories concerning on their origin but recently none of them is totally valid because the evolution of insect flight in particular lack the fossil evidence despite the fact that insects were the first group of organisms which have evolved the ability to fly. They were able to fly much earlier that the first flying vertebrates have appeared. Development of the wings brought many benefits to insects. Because of ability to fly, they were able to disperse, exploit new spaces, escaped from predators and they could better find sexual partner (Grimaldi & Engel, 2005).

Immature wings of Paleozoic Palaeoptera were articulated while in most recent nymphs the wings are firmly fused to the tergum (Kukalová-Peck, 1978, 1991, 2008). Wing articulations within all winged insects have been homologised by Kukalová-Peck (1983). She proposed that the most primitive type of wing articulation is densely crowded band of articulated sclerites surrounding the wing base. Basal sclerites are arranged in eight rows for delivering blood to the main wing veins; each row includes three sclerites (proxalare, axalare and fulcalare) articulating with basivenale, which also serves as blood sinus for one of eight

main veins (Kukalová-Peck, 1983, 1987, 1991). In all palaeopterans, with the only exception of the order Diaphanopterodea, several of these sclerites are fused to the articular plates which are fused to the bases of main wing veins thus preventing folding of the wings over the abdomen.

1.3.1 Wing tracheation

Insect wings are complex structures consisting of two epidermal layers interlaced by tracheae delivering blood, oxygen and nutrients (Needham, 1935).

Wings arise as an epidermal thickening located above the spiracle, and are separated from the tergum in young nymphs. During the development, the wing folds migrate towards the tergum and finally fused with it (Kukalová-Peck, 1978; Needham, 1935).

Comstock & Needham (1898-1889) studied the tracheation and homologized the wing venation between insect orders. They stated that principal tracheae precede the position of the main wing veins in immature wings.

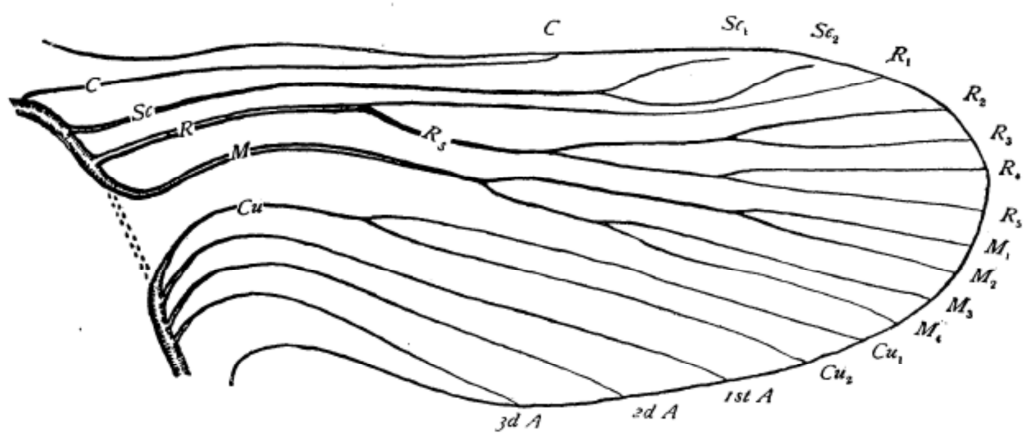


Figure 4. Hypothetical tracheation of a wing of the primitive nymph (Comstock & Needham, 1898-1899, part 2)

According to Needham (1935), the tracheae are the first structures growing out, and veins develop later above and below these tracheae. Thus, tracheae determine the position of main longitudinal veins (Comstock & Needham, 1898-1899).

While some authors have demonstrated considerable flexibility in the tracheal system in general (see Wigglesworth, 1954), other works have shown stability of the basic components. Landa (1948) have found extensive homologies within the order Ephemeroptera.

The work of Comstock & Needham (1898-1899), summarized in Comstock (1918) based on the tracheal supply to the wings form the basis of most modern schemes of nomenclature. Comstock & Needham (1898-1899) were convinced that tracheation pattern reflect the position of wing veins and that the number of branches to each main longitudinal vein is known, thus the veins could be named and homologized. However, according to Holdsworth (1940), the tracheae enter the wing pads after the lacunae established the position of the veins and thus tracheae actually do not determine the position of the veins. Lacunae in immature wings are free spaces surrounded by epidermal cells forming the veins above and below these lacunae (Kukalová-Peck, 1978). Thus lacunae represent veins precursors. Also Whitten (1962) have demonstrated in his study that wing tracheation may vary not only among individuals, but even between instars of one individual. Carpenter (1966) have summarized the evidences refuting the assumption about tracheae preceding the position of the veins.

Already in newly hatched insect nymph the basic tracheation pattern is established and prior to the first molt, the new tracheal intima is laid down around the old one. Old intima will later break, and its two portions will be removed in association with their respective spiracles (Whitten, 1962). Several modes of formation of new tracheae are captured in figure 5. According to Wigglesworth (1954), the wing tracheae may also increase in number at each ecdysis, and new ones may arise in areas with deprivation of oxygen.

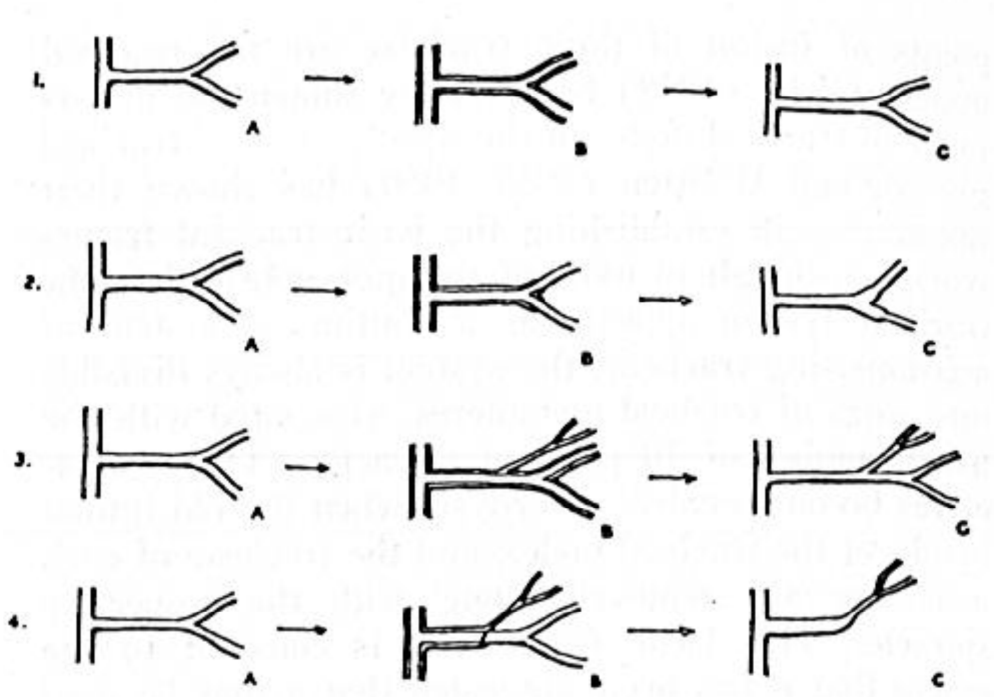


Figure 5. Methods of formation of new tracheae, so far determined in insects. 1. Straight forward development. The intima of the new trachea is secreted around that of the old (B). The old is removed at the molt leaving the appearance as in C. 2. The finer branches are retained, whilst the larger branches are replaced. The new intima fuses with the old at the point where the break will occur in the old (B). Parts proximal to this will be removed at the molt: parts distal to this point will be retained. A "step" may be discernible in the next instar where the break has occured (C). 3. Formation of new brach trachea. The old tracheae are replaced, and at the same time the tracheal epithelium forms a new branch. The new intima of this, when secreted, will be continous with the new intima secreted around the old main branch (B). After the molt the appearance will be as in C. 4. Formation of a new branch trachea with no replacement for the distal portion of the main trachea. Here a new branch is formed as in 3: no new intima is secreted around the original distal trachea (B). At the molt the old intima is removed, the "hole" in the new tracheal lining is "sealed" over by tracheal epithelium, and the distal epithelium is histolysed. In studies of tracheation, the subdivisions of A of one instar might be homologized with those of C of the next, unless the development were unknown (Whitten, 1962)

In most insects, the wings are served by two basal tracheae: anterior and posterior. Anterior basal trachea of each wing gives off the tracheae of the costal, subcostal, radial and medial veins while the posterior one gives off the cubital and anal tracheae (Yadav, 2003). Anterior basal trachea of the fore wing arises from mesothoracic spiracle, the posterior basal trachea from metathoracic spiracle. Two basal tracheae supplying the hind wing arise from the metathoracic and first

abdominal spiracles (Kukalová-Peck, 1978). The order Ephemeroptera represents an exception because ephemeropteran wings are served by only a single basal trachea (Hamilton, 1971).

Tillyard (1915) reported about development of the wing venation in zygopterous dragonfly *Diphlebia lestoides* (Selys, 1853) and found out that the basic difference between Anisoptera and Zygoptera is condition of the radius, which has a single branch in all Anisoptera while in Zygoptera is unbranched. Also, in Anisoptera M gives off three branches, while in Zygoptera M gives off four branches.

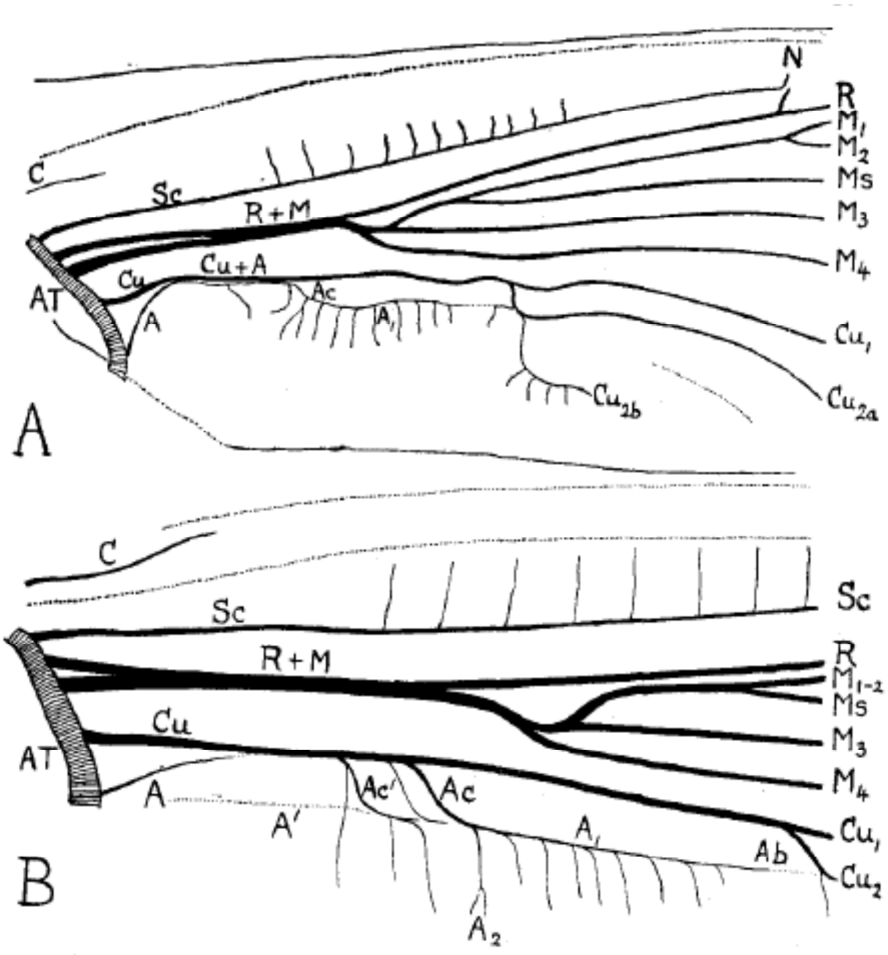


Figure 6. Tracheation of larval wing of *Diphlebia lestoides*. A. Antepenultimate instar; B. Penultimate instar (Tillyard, 1915).

There are many deviations in tracheation pattern among insect orders, but all these modifications may be derived from the fundamental simple plan in which two tracheae enter the wing base (Yadav, 2003). It follows, that tracheation pattern in nymphal wing pads is not immutable. Tracheae in the wing pads cannot be taken as fundamental in determining the homologies of the wing veins. It may, however, be an excellent guide thereto in so far as the main tracheae normally pass along the lacunae that precede the veins in the wing pads.

1.3.2 Wing venation

Wing venation consists of at least eight main longitudinal veins arising from each basivenalia: precosta (PC), costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), anal (A) and jugal (J). These veins were originally composed of two sectors, convex anterior and concave posterior (e.g., media anterior MA+; media posterior MP-), separating near to the wing base. Later these two sectors became adjacent and finally fused into the common stem (Kukalová-Peck, 2008). For efficient flying, the wings required amplified anterior wing margin which have formed by fusion of PC, CA, CP and ScA. These four veins are still separated in many fossils (Kukalová-Peck, 1991).

Insect wing is a key evolutionary innovation for insect radiation but its origins and intermediate forms are absent from the fossil record. Evolutionary origin of insect flight is a popular topic for study (Kukalová-Peck, 1978) and because there are no known fossils of the earliest stages of winged insect, informations concerning on this topic must be drawn from fossils, physical models of insects or from living insects (Marden, 2003).

A number of hypotheses have been proposed to explain the wing origin (Wigglesworth, 1973; Kukalová-Peck, 1978; Rasnitsyn, 1981; Grimaldi & Engel, 2005). These hypotheses about morphological origin may be divided into two major classes - the first one suggested that wings are new structures not homologous with any other structures and the second suggested that wings are

transformed old structures (Hamilton, 1971). Each of wing origin hypotheses has some merits and demerits which will be discused bellow.

1.4 Hypotheses concerning the origin of insect wings

1.4.1 Paranotal theory

In the past widely accepted and quite popular paranotal theory, also known as 'flying squirrel theory' (Müller, 1873), originally advanced by Woodward (1876) proposes that insect wings are entirely new structures, originated from solid lateral outgrowths of thoracic segments (Bradley et al., 2009, Crampton, 1916, Douglas, 1980, Grimaldi & Engel, 2005).

This theory is supported by Snodgrass (1935), Sharov (1966), Hamilton (1971, 1972) Wootton (1976) and Rasnitsyn (1976, 1981).

According to this hypothesis, the wings have evolved from nonarticulated lateral extensions of the thoracic terga and initially served as gliding planes (Hamilton, 1971). The ability to glide was very important, mainly at the beginning of the evolutionary period because the flight was imperfect, wings beat slowly and gliding was the most economical way to gain height and to disperse (Kukalová-Peck, 1978). According to paranotal theory, the gliding planes must have been primitively developed on all three thoracic segments and their shape was thought to have resembled the prothoracic paranota of the Palaeodictyoptera and the mesothoracic and metathoracic wing buds of immature winged insects (Hamilton, 1971).

Later, the wings became enlarged, flattened and acquired a line of flexion permiting the flapping motions (Wootton, 1976). When the wing articulation began to form, the insects were able to control the aerial descent from perches on tall plants (Grimaldi & Engel, 2005). Hasenfuss (2008) reported that climbing on plants and descending from there by falling down and gliding has led to the movability of primitively immobile paranota.

Paranota occured already in Arthropoda, protecting the sides of the body (Kukalová-Peck, 1978) and therefore it is generally assumed that the insect wings have evolved as follows: initially the protective thoracic paranota became gradually enlarged and served first as parachutes during descent, later they acted

as gliding surfaces and ultimately as flapping aerofoils (Wootton, 1976, 1981). According to this theory, the insect wings originated from primitively immobile thoracic extensions (Jockusch & Ober, 2004) which probably became movable by desclerotization along a tergal area (Hasenfuss, 2008).

The paranotal theory has several merits and demerits. Well developed paranotal lobes with venation pattern similar to miniature wings, occuring on the prothoracic segments of some Paleozoic insects (for instance some members of the order Palaeodictyoptera considered by Hamilton, 1971), were regarded to be the most critical evidence supporting this theory (Grimaldi & Engel, 2005). The other evidence favoring the paranotal theory is derived from development of wing pads in immature winged insects (Hamilton, 1971) and flatness of the wing and its position in the boundary of the tergum and pleuron is consistent with this hypothesis (Niwa et al., 2010). A wing primordium is fused with the tergum during the development of hemimetabolous insects, which is also regarded to be one of main evidences supporting this theory (Jockusch & Ober, 2004).

On the other hand, paranotal theory is not able to explain the origin of muscles, there is no evidence for an articulatory wing hinge characterizing the attachment of the paranotal lobes to the thorax, thus disallowing flapping movements (Labandeira, 1999; Niwa et al, 2010) and prothoracic lobes of any recently known fossils were not articulated (Grimaldi & Engel, 2005).

Paranota are described in crustaceans (Crustacea), myriapods (Myriapoda) and trilobites (Trilobitomorpha), they are typically evolved on the terga of wingless insects (Kukalová-Peck, 1978) and generally they occured on the terga of strongly dorsoventrally flattened insects, probably concealing them from predators (Hamilton, 1971). These structures were quite primitive, often with distinct venation pattern and in some cases even with a developed hinge so they could move up and down to some extant (Kukalová-Peck, 1978).

Primitively immobile paranota may have diverse function; they may have originally functioned as sex attractants (Alexander & Brown, 1963), as thermoregulators (Douglas, 1980) or as stationary aids in aerial migrations of small insects (Rasnitsyn, 1981).

In the past, these lateral structures occured on all three thoracic segments as wings and on nine abdominal segments as winglets (Kukalová-Peck, 1983). According to Kukalová-Peck (1978), the paranotal theory is not valid because paranotal lobes are described as lateral outgrowths of the thoracic terga thus they should be primitively continuous with the tergal plate and well sclerotised, however the lateral abdominal structures in primitive Paleozoic insects were separeted by a suture (Kukalová-Peck, 1978).

According to Kukalová-Peck & Peck (1976), all primitive Paleozoic insect nymphs had articulated and freely movable wing pads which lost their movability by fusion with the tergum and thus became convergent with paranota. Fossil record do not provide any evidence indicating that paranotal theory is valid. All described Paleozoic nymphs had articulated and functional wings and if this movability and articulation was known to paleoentomologists, how is it possible that Sharov (1966), Wootton (1976) and Rasnitsyn (1976) supported the paranotal theory?

Sharov's support for this hypothesis stemmed from wrong classification. He suggested that uropods of Devonian crustacean *Eopterum devonicum* Rodendorf 1961 were the wings of ancient winged insects. Wootton (1976) and Rasnitsyn (1976) studied only the nymphs of Palaeodictyoptera and they had not the opportunity to examine the others Paleozoic palaeopterous insects. Some of palaeodictyopterous nymphs were rather peculiar, heavily sclerotized and thus the function of their wings was reduced due to this specialization (Kukalová-Peck, 1978).

The paranotal theory is generally supported by the group Zygentoma, because silverfish possess distinct tergal expansions which can be used for controling the descent while falling (Hasenfuss, 2008, Jockusch & Ober, 2004).

Kukalová-Peck (1983) rejected the possibility that the insect wings have evolved from immobile lateral extensions of the thoracic terga and that they were of tergal origin. She supposed that ancestral forms had completely movable wing pads, while descendants had firmly attached wing pads. The wing pads of modern nymphs are secondarily fused with the tergal margins, thus incapable of

movements and therefore nymphal wings and paranotal expansions had never anything in common (Kukalová-Peck & Peck, 1976).

1.4.2 Epicoxal theory (Limb branch theory)

This hypothesis, also called ‘limb branch hypothesis’ or ‘exite theory’ was originally introduced by Wigglesworth (1973, 1976) who supposed that insect wings are homologous with the abdominal gills of mayfly nymphs and with the abdominal styli of wingless insects (Kukalová-Peck, 1978).

This theory is more consistent with fossil evidence than paranotal theory and Paleozoic insect nymphs are often used by Kukalová-Peck (1978, 1983) to support the epicoxal theory.

The limbs of primitive arthropods were eleven-segmented and some of leg segments beared various appendages. Dorsally located appendages are called exites while ventrally located appendages are called endites. It is assumed that the insect wings have evolved from limb exites which probably initially served as external gills and this persisted in many crustaceans until present time. Although the insect limbs are unbranched, members of basal wingless order Archaeognatha possess branched limbs (Jockusch & Ober, 2004).

According to this theory, the wings are of pleural origin and are serially homologous with abdominal gills of immature stages of Ephemeroptera (Kukalová-Peck, 1991). The gills are regarded to be modified exite of basal leg podit, called epicoxa (Kukalová-Peck, 1978, 1983, 1985, 1987). Epicoxa is more proximal of two subcoxal leg segments and it is considered to form the junction between the pleuron and the thoracic dorsum (Grimaldi & Engel, 2005).

In ametabolous and also in hemimetabolous insects, the limbs develop from limb buds which are located on a ventral side of the segment while in some holometabolous insects the limbs arise from imaginal precursor cells (Angelini & Kaufmann, 2005).

In basal hexapods, the limb buds are developing on all three thoracic and nine abdominal segments. Abdominal limb buds later often degenerate while the thoracic ones further develop (Bitsch, 2012).

It is possible that the insect wings have evolved from initially mobile gills in aquatic forms (Wigglesworth, 1973; Kukalová-Peck, 1983) or alternatively from structures derived from legs in terrestrial forms. The wings developed laterally from these appendages, termed as epicoxal exites and were articulated to the pleuron, which is fundamental difference from paranotal theory (Bradley et al., 2009).

Nymphs of Paleozoic mayflies possessed paired gills on abdominal segments and some authors suggest that these gills were homologous with the thoracic wings. They assume that because of the similar position of the wings and gills on the segments and because of tracheation pattern (Kukalová-Peck, 1978; Brodsky, 1994).

Unlike the paranotal theory, the epicoxal theory propose that wings were primitively movable, they arose as pleural structures and then migrated more dorsally, finally fusing with the tergum (Bitsch, 2012) thus forming the tergal lobes (Hasenfuss, 2008). When the wings fused to the terga, the metamorphic instar occured (Kukalová-Peck, 1983).

Kukalová-Peck (1987) also assumes that the nymphs of the ancestors of winged insects left the water, adapted to the terrestrial life and evolved the flight ability. Their gills were large enough for creating water currents but they were not as large as they could serve as airfoils. Due to that, some entomologists suggest that skimming on the water surface by wind, occuring in some Plecoptera, is an intermediate stage (Hasenfuss, 2008). This statement is a part of other hypothesis regarding the insect wing origin and will be disscused later.

Currently, there exist several evidences supporting this theory. One of the most important evidences is the position of the wing in the membrane between epicoxa and subcoxa (Kukalová-Peck, 1983) and equally important are probably studies performed on *Drosophila melanogaster*, Fallén 1823. During the development of *Drosophila*, the limb and the part of the wing of each segment are forming in the

same primordium and the wing primordium is then separating and migrating dorsally (Cohen et al., 1993). This hypothesis is supported by results from molecular genetics research. If the wings derived from dorsal appendages of multibranched limbs, it is supposed that in these homologous structures there are activated homologous genes (Averof & Cohen, 1997). Damen et al. (2002) studied two developmental genes *pdm/nubbin* (pdm/nub) and *apterous* (ap) and their results support the hypothesis that the wings evolved from ancestral arthropod gills (Wigglesworth, 1976; Kukalová-Peck, 1991).

Some authors, however, suggest that limb specification mechanisms described for *Drosophila melanogaster*, Fallén, 1823 may not be representative of insects in general (Angelini & Kaufmann, 2005; Jockusch & Ober, 2004). *Drosophila* belongs to the insects withi holometabolous type of development thus it undergo dramatic metamorphosis and entire adult ectoderm is formed from imaginal discs. Jockusch & Ober (2004) suggest that its development is partly different from that of other insects and the best way how to find out whether this character is ancestral for the whole grup is to examine that character in broadly sampled representatives of the group.

1.4.3 Modified paranotal theory

Although the paranotal theory was originally widely accepted, Jarmila Kukalová-Peck (1978) rejected the origin of the wings from the paranotum and she established her own theory (Rasnitsyn, 1981).

Kukalová-Peck (1978) assumed that wings are of the pleural origin. According to this hypothesis, the wings are appendages of the subcoxa, serially homologous to abdominal gills of Paleozoic Ephemeroptera (Komatsu & Kobayashi, 2012).

Kukalová-Peck (1978) suggested that the pro-wings were movable, they have complete articulation, obvious venation, and distinctly corrugated surface long time before the flight have evolved. The function of these preflight wings was diverse; they served for ventilation or closing spiracles, for retaining water, as a gill protection or they had locomotor function.

These pro-wings could have been inherited from aquatic arthropods ancestral to insects. Much later, after the flight had evolved; in Late Silurian and Early Devonian; the wings of immature stages temporarily fused to the terga. This fusion served as an adaptation to movement within shelters and among plants.

This theory is extremely attractive because it permits continuity in the evolution of insect wings as locomotory organs and the homology of the insect wings and the gills of Ephemeroptera also seems to be reliable. Although Grimaldi & Engel (2005) proposes that insect wing composed of two layers is partly derived from tergum and pleuron, Kukalová-Peck (1978) believes that the nymphs of Paleozoic insects had permanently movable wings during their ontogenetic development and therefore she rejected the assumption that insect paranota consists of tergal and simultaneously pleural components. However there is no evidence supporting this theory in the present time (Rasnitsyn, 1981).

Kukalová-Peck (1978) reconstructed the wing bases of two Dictyoneuridae (Palaeodictyoptera) and she found out that structure elements of the wing base in Palaeoptera differ from that of Neoptera. This statement is however in contrary to Brodsky (1974) who found structure and muscles of mayfly wings which are typical for Neoptera.

1.4.4 Surface-skimming theory

New theory regarding the insect wing origin was originally advanced by Marden & Kramer (1994) and gradually have gained considerable support.

The surface-skimming hypothesis supposed that insects primitively used their wings and aerodynamic motion for moving across water surfaces (Thomas et al., 2000). This assumption is based on the fact that skimming is generally widespread among Plecoptera and it is retained in the orders Ephemeroptera and Odonata thus it is possible intermediate stage between swimming and flying (Marden & Kramer, 1994; Marden, 2003). Some members of Plecoptera use for skimming all six legs (Taeniopterygidae, Nemouridae, Capniidae), the other use only mesothoracic and metathoracic pair of legs (Grypopterygidae), some of them skim

using only their hind legs (Leuctridae) and the rest is even able to jump from the water (Notonemouridae, Chloroperlidae, Perlodidae; Marden, 2003).

This theory propose that insects have evolved from semi-aquatic ancestors (Marden, 2003), although the most basal order of wingless insects Archaeognatha are fully terrestrial and thus some authors suggest that ancestor of winged insects was also terrestrial (Grimaldi & Engel, 2005).

There was no phylogenetic analysis showing that skimming is an ancestral condition rather than taxonomically isolated loss of wings and there is no analysis supporting the assumption that the flight apparatus in Plecoptera is plesiomorphic (Will, 1995).

Thomas et al. (2000) made phylogenetical analyses which indicated that the family Nemouridae is the basal clade of Plecoptera and because the surface skimming is widespread among the family Nemouridae and also in other families assigning to the superfamily Nemouroidea, it is possible that skimming ability is a retained ancestral trait.

It was examined that velocity of skimming increases with the inceasing temperature (Marden & Kramer, 1994) and that stoneflies keeping their abdomen in contact with water surface achieve the lowest velocity while plecopteran members raising the entire body above the water achieve the highest velocity (Marden, 2008).

According to Kukalová-Peck's (1987) assumption that insects have evolved from aquatic ancestor some authors suggest that skimming occuring in some Plecoptera is an intermediate stage (Hasenfuss, 2008). However it is difficult to find out if this statement is valid for insects in general (Marden, 2003). Some authors concluded that skimming locomotion descended from flight rather that preceded it (Rasnitsyn, 2003).

In the wing articulation of extant mayflies there is desclerotized platform allowing horizontal movements of the wings, which is necessary condition for skimming (Ruffieux, 1998). Brodsky (1994) assumes that this wing articulation pattern have existed already in the first winged insects.

Although this theory provides logical explanation, recently there is still lack of evidences supporting the surface-skimming hypothesis and it is very hard to find out how the insect wings evolved because there are unknown fossils of the earliest stages of winged insects (Marden et al., 2000; Wootton & Kukalová-Peck, 2000). Disadvantage of this hypothesis is the fact that first known winged insects were large or very large and first small fliers have appeared up only in the Carboniferous (Rasnitsyn, 2003). On the other hand, weight of skimmers is supported by water thus they could have achieved effective aerodynamic locomotion even with the small wings and weak flight muscles (Thomas et al., 2000). Evidence supporting this theory is presence of insects possessing gills and wings in the Upper Carboniferous and Lower Permian (Marden, 2003). These insects are regarded to be early stages in the evolution of surface skimmers and such fossils are abundant (Kukalová-Peck, 1991) and according to this hypothesis the wings and gills could have coexisted.

1.5 Paleozoic Ephemeroptera, Odonatoptera and Palaeodictyoptera

As it was mentioned above, orders Ephemeroptera and Odonata are the only ones recently representing the group Palaeoptera. These two orders of winged insects have aquatic nymphs and for this reason it was formerly frequently assumed that insects have evolved from some aquatic ancestor (e.g., Handlirsch, 1908). But this assumption is recently regarded to be probably invalid because nymphs of the most basal members of wingless insects (Archaeognatha and Zygentoma) are not aquatic, and fossil record indicates that insects colonized freshwater ecosystemes roughly 200 million years after their origin (Bradley et al., 2009).

According to Kukalová-Peck (1987), arthropod ancestor was aquatic, with movable gill plates similar to the gill plates of Ephemeroptera, and she regarded these ephemeropteran gills to be serially homologous to the insect wings (Brodsky, 1970, 1974). However, Kukalová-Peck (2008) later rejected her own assumption of aquatic ancestor.

The order Ephemeroptera is considered by some authors to be the most basal order of winged insects living today. The wing base of mayflies is primitive, consists of a single sclerotized plate and all of the veins arise from there (Hamilton, 1971; Yoshizawa, 2007).

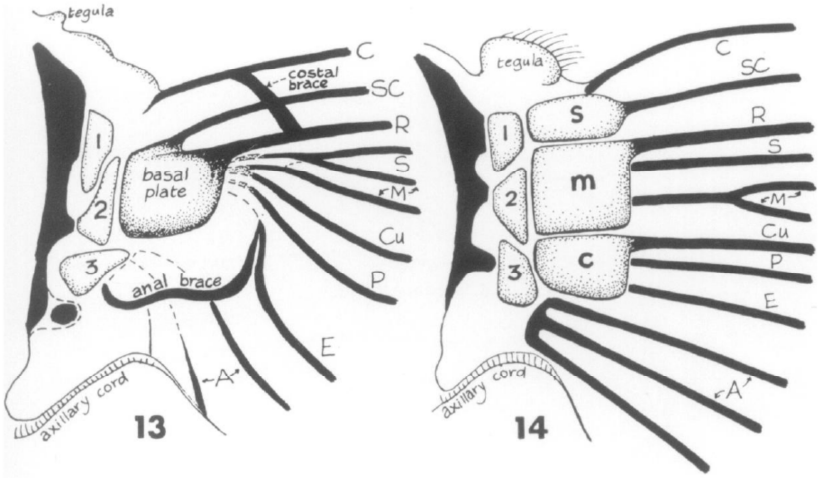


Figure 7. Basal sclerites of wings. A. Ephemeroptera (Heptageniidae); B. Theoretical ancestral type (Hamilton, 1971).

Palaeozoic mayflies were noticeably different from recent members of the order Ephemeroptera. During the Paleozoic they had well developed all six legs while recent ones have reduced mesothoracic and metathoracic legs. Also, forewings in recent Ephemeroptera are much larger than hind wings, but in the course of Paleozoic the wings were similar in size (Carpenter, 1992). Next differential character is in the wing attachment, which is very broad in modern ephemeropterans and wing articulation is not distinct while in Paleozoic mayflies the wings were narrowly attached and distinctly articulated (Hubbard & Kukalová, 1980).

Figure 8. *Protereisma* sp. (nymph no. 1), Lower Permian of Oklahoma, original drawing, claws of left middle leg and right hind leg figured from dorsal view (Kukalová, 1968).

Nymphs of Paleozoic mayflies were also remarkably different from the recent ones. Their wing pads were attached to the terga differently from the way in which they are attached in recent nymphs (Kukalová, 1968). Postembryonic development of Paleozoic Ephemeroptera was similar as in Palaeodictyoptera and will be discussed later (Kukalová-Peck, 1991).

Order Odonatoptera, comprising the recent dragonflies and damselflies along with the extinct griffenflies and others, is similar as Ephemeroptera considered as one of the oldest lineages of winged insects (Kukalová, 2009; Engel, 2013). They have attained enormous body proportions. According to Grimaldi & Engel (2005), the largest insect ever was dragonfly *Meganeuropsis permiana* Carpenter, 1947 known from the Early Permian of Kansas, Oklahoma (wing span approximately 710 mm).

Wing base of odonatopterans consist of two articular plates: costal plate and radio-anal plate (Kukalová-Peck, 1991). In articular plates, the individual sclerites are still separated and partly movable in Protodonata, while in Odonata they are completely fused.

Odonatoptera and Ephemeroptera have their wings permanently spread due to fusion of several basal articular sclerites into articular plates which are fused to the basis of main longitudinal veins (Kukalová-Peck, 1991; Bechly et al., 2001).

Although adult wing fragments are quite common in Late Carboniferous and during the Permian, fossil nymphs of Odonatoptera are extremely rare (Kukalová-Peck, 2009).

Order Palaeodictyoptera have been established for the palaeopterous insects of rather large size known from the Upper Carboniferous and Permian (Carpenter, 1992). They were remarkably diversified from earliest Late Carboniferous to the Late Permian, comprised one of major insect orders (Grimaldi & Engel, 2005).

Palaeodictyopterans were characterized by small hypognathous head, haustellate beak adapted for obtaining cell sap from plant tissues, by prothorax bearing paired triangular winglets protruding laterally, with specific venation pattern, and by wings held in outstretched position (Beckemeyer, 2000; Kukalová-Peck, 1974; Kukalová-Peck, 1978).

Unlike the orders Ephemeroptera and Odonatoptera, in Palaeodictyoptera it is generally assumed that nymphs were terrestrial because they have shown no adaptations for aquatic life (Sinitshenkova, 2002a; Carpenter & Richardson, 1968, Carpenter, 1992, Wootton, 1972).

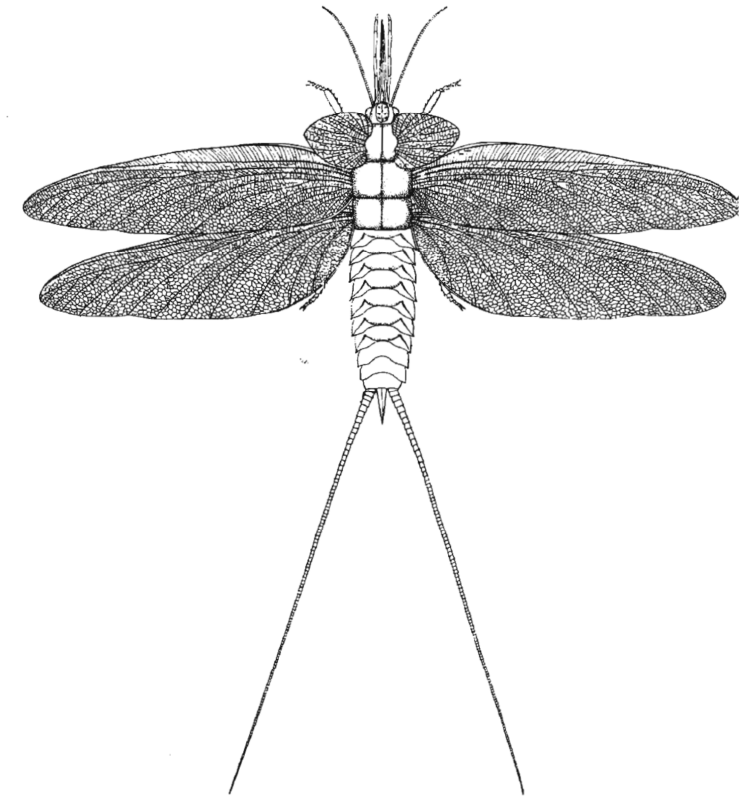


Figure 9. Reconstruction of *Stenodictya lobata* (Brogniart, 1890) based on several specimens (Kukalová-Peck, 1970).

They were hemimetabolous, but their development have differed from the development of recent hemimetabolous insects. All recent winged insects have in their development one to several metamorphic instars in which the wings are dramatically increasing in size and wing articulation is formed, but in Palaeozoic Ephemeroptera, Odonatoptera and Palaeodictyoptera the metamorphic instar was missing (Kukalová, 1978). Their development was gradual and required many nymphal and subimaginal instars. It is assumed by some authors, that older nymphs were probably able to fly (Kukalová-Peck, 1991, Sinitshenkova, 1979). Immature wings of the most of recent nymphs are firmly fused with the thoracic

terga, with the exception of dragonflies (Odonata) and grasshoppers (Orthoptera) whose wings are partly movable and some Plecoptera which have wings still separated from the terga by sutures (Kukalová-Peck, 1991). Unlike recent nymphs, immature wings in Paleozoic Palaeodictyoptera and Ephemeroptera were articulated to their respective thoracic segments and were arched backwards (Kukalová-Peck, 1978).

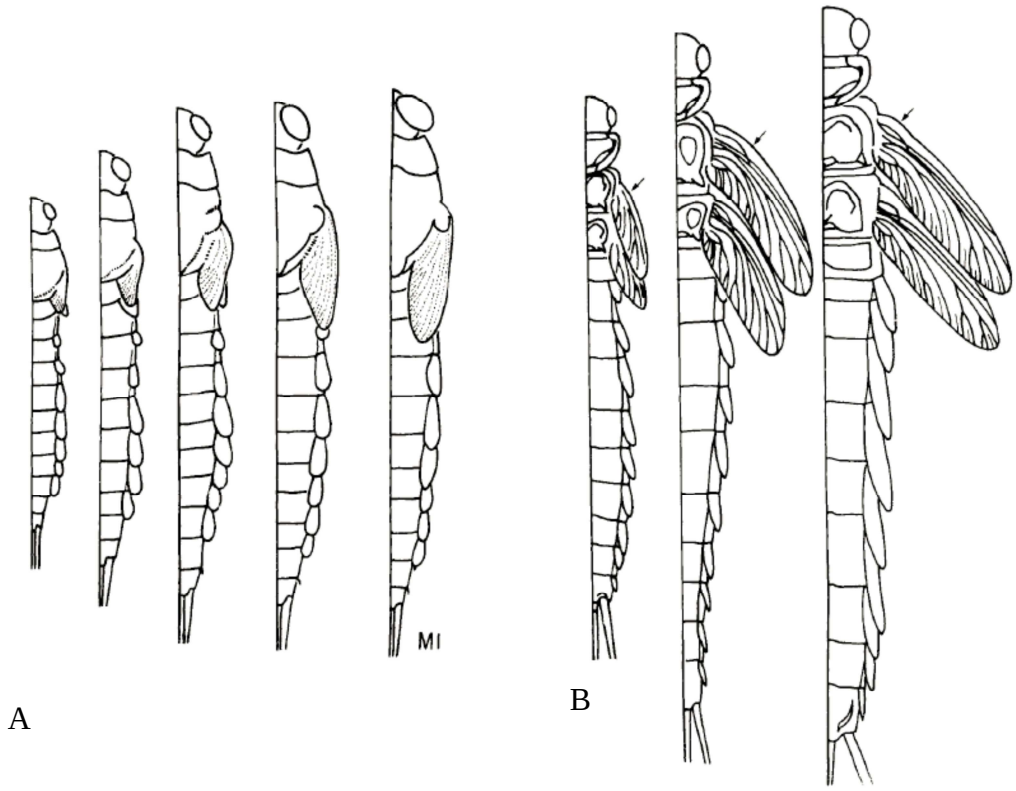


Figure 10. A. Metabolous development in Recent primitive mayflies (Siphlonuridae), shortened and schematized. Wing pads are secondarily fused with the terga and suppressed in size; articulation, venation, and adult size are recovered during the metamorphic instar (MI); B. Ametabolous development typical for Paleozoic mayfly nymphs (Kukaloviidae); wings were neither fused nor suppressed in size, but were articulated, veined and functional in forward position; the wings were streamlined by being curved backwards by a nymphal wing bend (arrows) which gradually straightened in each subsequent older instar until the alar axis became perpendicular to the body in the adult (not shown); the metamorphic instar was not present because it was not “needed”; Lower Permian, Czech Republic (Kukalová-Peck, 1991).

Initially small, distinctly veined, posteriorly curved nymphal wings became longer and straighter in each following instar until the wings were completely outstretched (Sinitshenkova, 1979). Similar wing development have been

demonstrated for the Calvertiellidae (Palaeodictyoptera; Kukalová-Peck & Peck, 1976).

Adults of Paleozoic Ephemeroptera and Palaeodictyoptera had almost straight anterior margin of the wings, thus immature wings were easily distinguishable due to prominent keel which became straightened after each molt, and have completely dissappeared in adult wings (Kukalová-Peck & Peck, 1976).

Our recent knowledge regarding on immature wings of Palaeodictyoptera are not sufficient due to lack of suitable fossils. It is also very complicated to associate palaeodictyopteran nymphs with adults because of venation pattern in the immature wing is only partly developed (Carpenter, 1948; Carpenter & Richardson, 1971).

1.6 Immature stages of Paleozoic Ephemeroptera, Odonatoptera and Palaeodictyoptera

1.6.1 Immature stages of Palaeodictyoptera

In 1948 there were five palaeodictyopterous nymphs described, four of them by Handlirsch (1906) and one by Goldenberg (1873). All of them were from Upper Carboniferous strata. Although few Carboniferous nymphs were known, it was very difficult to associate them with adults. It is possible to associate them on the level of the family or order but further placement is not possible. The principal problem is that these nymphs belong to extinct order. In fossils, which are members of some existing order, the association can be made with near certainty because comparison with living adults is possible.

Carpenter (1948) considered the current knowledge of immature Carboniferous insects insufficient and regarded the position of nymphs described by Handlirsch (1906) and Goldenberg (1873) obscure, so he assigned these nymphs to Insecta *Incertae Sedis*.

Woodward (1913) described *Rochdalia parkeri*, Woodward, 1913 from the Lower Coal Measures of Sparth Bottoms, Rochdale, Lancashire, UK. He was convinced that this specimen belongs to Branchiopoda (Crustacea). Following authors associated *Rochdalia* with the shrimps or Anostraca. Hutchinson (1930) established *Rochdalia* the type genus of a new family Rochdalidae and included it in his order Palaeanostraca, Stermer (1944) assigned *Rochdalia* to his Trilobitomorpha.

Later restudy of this specimen housed in Manchester Museum have shown that *Rochdalia* is an insect nymph. It was reported that this fossil possessed wing pads with distinct concave venation, terminal annulated cerci, and ten-segmented abdomen with the last segment forming a triangular process between the cerci (Rolfe, 1967).

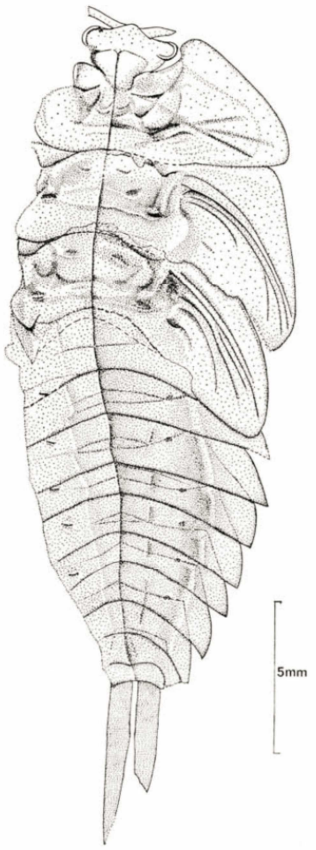


Figure 11. *Rochdalia parkeri* Woodward, manchester Museum L.11464, drawing is based on the convex impression, but includes details, particularly of the head and wing pads, derived from the counterpart (Wootton, 1972).

Later work made by Carpenter and Richardson (1968), Kukalová (1968, 1969a, 1969b, 1970), Sharov (1971) contributed to confirm the position of *Rochdalia* nymph in the order Palaeodictyoptera, because it has several characters that supports its attribution to the Palaeodictyoptera. These are the form of the prothoracic paranota, the abdominal paranota and the cerci which are widespread among Palaeodictyoptera. The other described nymph was *Idoptilus onisciformis*, Wootton, 1972. There was preserved less of the body than in the case of *Rochdalia parkeri*, but some surface details were clearer. On the basis of wing pad venation this specimen was assigned to the Palaeodictyoptera. On the wing pad there are MA and MP clearly convex and concave, and CuP and first anal vein of the hind wing are strongly curved. In most Neoptera the median veins are

flat and in all Polyneoptera CuP and first anal vein are straight, so these characters indicate that *Idoptilus* can be assigned to Palaeodictyoptera.

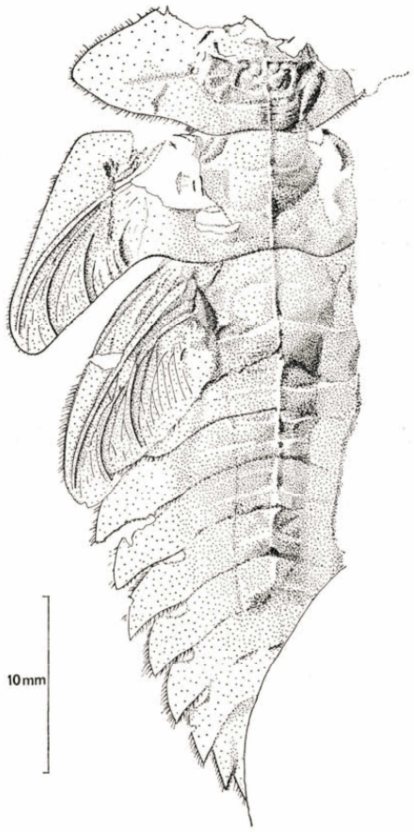


Figure 12. *Idoptilus onisciformis* n. gen. n. sp. British Museum (Natural History), drawn by tracing photographs taken by oblique light (Wootton, 1972).

Although neither *Idoptilus* nor *Rochdalia* are demonstrably terrestrial, they do not show any aquatic adaptations (Wootton, 1972).

Kukalová (1969a, 1969b, 1970) rediscribed all palaeodictyopteran taxa from Commentry, France. That was found the best preserved collection of this order and she provided detailed study of these fossils and showed that extinct order Palaeodictyoptera was considerably diverse.

She studied the projections of ththorax and abdomen which occur in almost all Megasecoptera and in some Palaeodictyoptera. These projections were at the beginning considered as tracheal gills that persisted into the adult stage and later were interpreted as short lateral spines on the thorax and abdominal segments.

Gill-like structures were denied by Lameere (1917). Martynov (1938) have characterized order Megasecoptera as group of insects with lateral expansions of abdominal segments with tooth-like or spine-like outgrowths and he considered these outgrowths to be homologous with prothoracic spines and winglets of Palaeodictyoptera, although reduced and modified. Carpenter (1951) determined these projections as extensions of tergites. After the research made by Carpenter & Richardson (1968) on megasecopterous nymph, *Mischoptera douglasii* Brogniart, 1893, the processes were considered as hollow outgrowths of the tergites usually arranged into regular transverse rows, and were simple or branched from short to very long. These structures are unique in the two insect group Megasecoptera and Palaeodictyoptera and their function remains unclear (Kukalová-Peck, 1972).

Carpenter and Richardson (1971) reported about the nymph *Lycodemas adolescens* Carpenter & Richardson, 1971, which is according to them 'the first unquestioned nymph of the order Palaeodictyoptera'. The nymph held its wing pads obliquely away from the body thus resembles the megasecopterous nymph, *Mischoptera douglasii* Brogniart, 1893, however the wing venation shows that this fossil is a member of the order Palaeodictyoptera and according to Carpenter & Richardson (1971) it probably belongs into the family Lycocercidae. However, this nymphs is strinkingly different from other palaeodictyopterous nymphs and the familial assignment is not very sure.

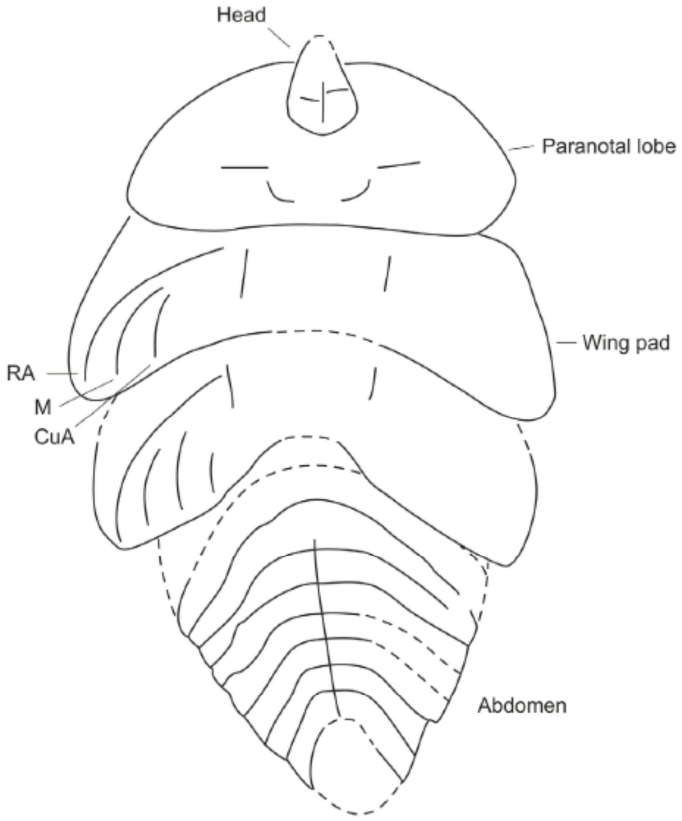


Figure 13. *Idoptilus peachii* (Woodward, 1887b) comb. nov., holotype. DI Ail; Middle Coal Measures (Westphalian B), Greenhill Quarry, Ayrshire, line drawing of specimen (Ross, 2010).

Sinitshenkova (1979) have studied the material of Carboniferous insects from the Tunguska Basin, Russia, and have reported several palaeodictyopterous nymphal wings. She have established the new family Tchirkovaeidae and attributed to the genus *Tchirkovaea* Zalessky, 1931 *Tchirkovaea guttata* Zalessky, 1931, and *Tchirkovaea sharovi* Sinitshenkova, 1979. Sinitshenkova (1979) also erected new genus *Paimbia* for *Paimbia fenestrata* Sinitshenkova, 1979.

Not long ago, the other palaeodictyopterous nymph *Idoptilus peachii* (Woodward 1887b) originally described as a cockroach nymph have been redescribed and attributed to the order Palaeodictyoptera (Ross, 2010). This onisciform nymph possess prothoracic lobes of nearly triangular shape, characteristic for the order Palaeodictyoptera, and wing pads with typically corrugated venation pattern. Although the wing venation is rather poorly preserved, convex veins RA, MA and CuA are distinct and strongly curved to the posterior wing margin.

Until recently, several palaeodictyopterous nymphs have been described. *Rochdalia parkeri* Woodward, 1913 and *Idoptilus onisciformis* Wootton, 1972 are known from the British Carboniferous Coal Measures, *Idoptilus peachii* (Woodward, 1887b) is known from Carboniferous of Scotland (Ross, 2010). All these onisciform nymphs have uncertain familial position, while *Lycodemas adolescens* Carpenter & Richardson, 1971, *Tchirkovaea guttata* Zalessky, 1931, *Tchirkovaea sharovi* Sinitshenkova, 1979 and *Paimbia fenestrata* Sinitshenkova, 1979 have been assigned to the certain palaeodictyopterous families and they are not of onisciform type. *Lycodemas adolescens* Carpenter & Richardson, 1971 is known from Pennsylvanian (Westphalian C/D) concretions of Illinois and the remaining three nymphs are from Carboniferous of Siberia, Russia (Sinitshenkova, 1979).

1.6.2 Immature stages of Ephemeroptera

Kukalová (1968) described six specimens of mayfly nymphs from Lower Permian in Moravia. These fossil mayfly nymphs described were placed into the family Protereismatidae which was established by Lameere (1917). One of these nymphs was found in Oklahoma (*Protereisma* sp., nymph no.1) while the remaining five specimens (nymphs no. 2, 3, 4, 5, 6) were collected in the Lower Permian of Obora, Moravia, in the Czech Republic.

Five nymphs were placed into the genus *Protereisma* but the sixht nymph was very different and its family position cannot be established.

The Permian protereismatid mayfly nymphs were adapted for aquatic life; they possess gills on the first nine abdominal segments (Kukalová, 1968).

Demoulin (1970) removed these described mayfly nymphs from the order Ephemeroptera and assigned them to the order Archodonata on the basis of presence of segmented tarsi, double tarsal claws, and details of the wing venation.

The same author placed the Permian nymph no.1 *(Kukalova americana*) into the new genus *Kukalova* and he also assigned nymph no. 3, 4 and 5 into this genus.

There was also established the new family Kukalovidae comprising the monotypic genus *Kukalova* Demoulin, 1970.

Hubbard and Kukalová-Peck (1980) have put these nymphs back to the Ephemeroptera and placed them into the superfamily Proteresmatoidea. In addition the family Kukalovidae was synonymized with Protereismatidae.

Later, Kukalová-Peck (1985) made a description of mayfly *Bojophlebia prokopi* Kukalová-Peck, 1985, which was found in the Central Bohemian Coal Basin of the Czech Republic and she also described the nymphs *Lithoneura piecko* Kukalová-Peck, 1985 and *Lithoneura clayesi* Kukalová-Peck, 1985. The genus *Lithoneura* Carpenter, 1938 belongs to the family Syntonopteridae Handlirsch, 1911 (Kluge, 1996). These two nymphs have been found in the middle Upper Carboniferous strata of Mazon Creek, Illinois, USA.

There are several differences between modern and Paleozoic mayfly nymphs. In modern ones the head is often hypognathous, antennae are short and thin and mouthparts are weak while in *Bojophlebia* the head is prognathous, antennae are thicker and mouthparts are well developed and adapted for feeding. In modern mayfly nymphs the largest segment of the thorax is the mesothorax while in *Bojophlebia* the metathorax is the largest one. Abdomen of modern nymphs bears seven pairs of gills while *Bojophlebia* has nine pairs (Kukalová-Peck, 1985).

This suggested ephemeropteran nymph was later separated from imago, and renamed as *Carbotriplura kukalovae* Kluge, 1996 and placed into the suborder Carbotriplurina in the order Thysanura (Kluge, 1996). *Carbotriplura kukalovae* has lateral projections on the abdominal, and also on the thoracic segments. Kukalová-Peck (1985) considered them to be the wing pads but on the thoracic paranota there are visible no veins so there is no reason to consider them wing pads. She was also convinced that lateral abdominal projections were tracheal gills but actually these projections are regarded to be paraterga (Kluge, 1996).

1.6.3 Immature stages of Odonatoptera

For the long time no Paleozoic nymphs belonging to the order Meganisoptera and Odonata was known thus it was not certain that Meganisoptera and earliest Odonata had aquatic juveniles (Wootton, 1981). Kukalová-Peck (2009) have described very rare fossil nymphs of Meganisoptera. She also established three genera; *Dragonympha* (*Dragonympha srokai*), *Alanympha* (*Alanympha richardsoni*) and *Carbonympha* (*Carbonympha herdinai*). The first two genera belong into the order Meganisoptera while the third genus is part of the order Eomeganisoptera. All of these nymphs are from Pennsylvanian (Late Carboniferous) and were found at Mazon Creek, Illinois, USA.

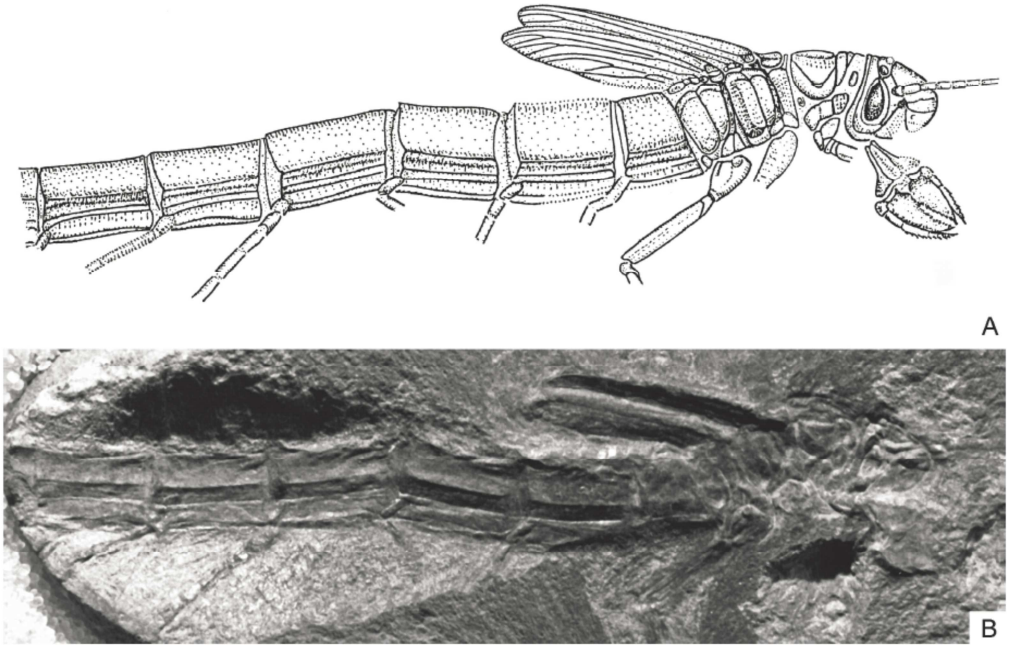


Figure 14. *Dragonympha srokai* n. gen., n. sp., holotype († Meganisoptera), young nymph of a large adult, wings uplifted (flexible, not fused to body) and streamlined with body, abdominal gills derived from segmented leglets, Pennsylvanian (Moscovian), Mazon Creek, Illinois, USA; A. Composite figure, obverse and reverse combined; B. Obverse of the holotype, uncoated, the end of abdomen missing. – Length of the remnant without antennae = 38.1 mm (Kukalová-Peck, 2009).

2. MATERIAL AND METHODS

2.1 Locality

Fossil specimens described in this thesis have been collected in Sosnowiec−Klimontów, originally Porąbka−Klimontów Mine, Upper Silesian Coal Basin, Poland.

The Upper Silesian Coal Basin (USCB) is a triangular sedimentary structure situated mainly in the Silesian part of Poland and partly in the north-eastern Moravia (Czech Republic). In this Coal Basin, over 60 coal mines were previously active, but Porąbka−Klimontów and Sosnowiec are abandoned for about 10 years (Gzyl & Frolik, 2005).

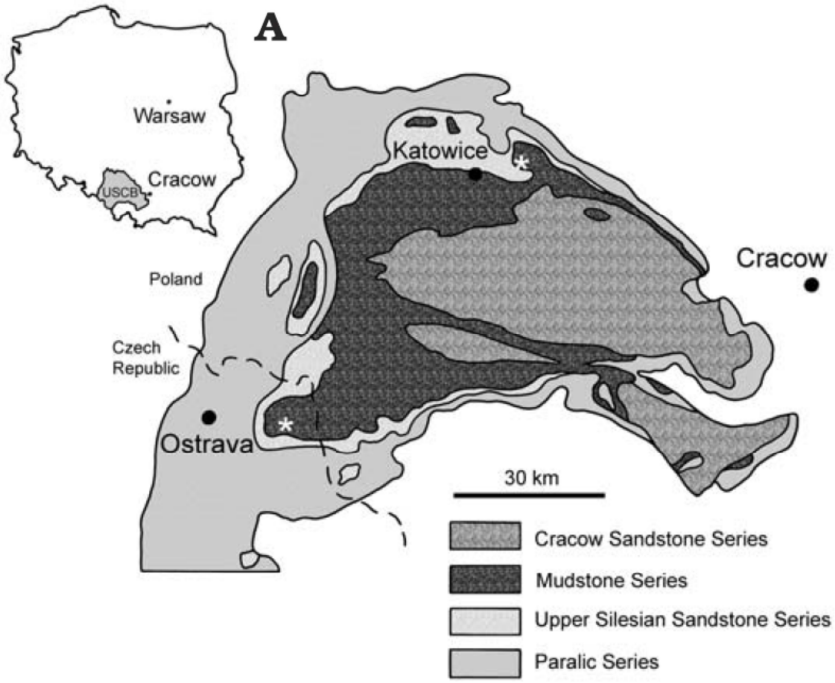
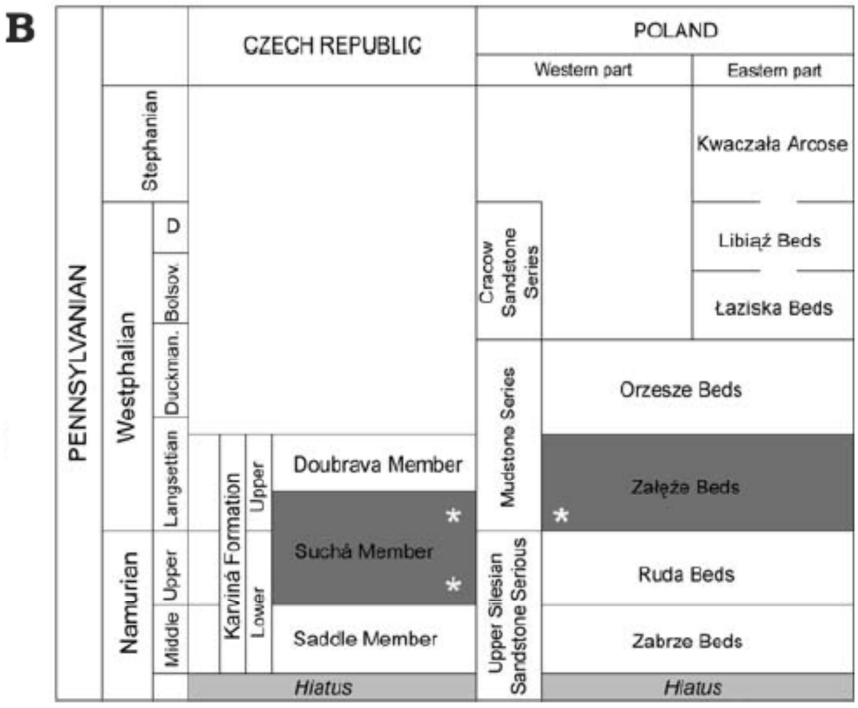


Figure 15. A. Geographical situation and geological map of the Upper Silesian Coal Basin with position of insect localities: Horní Suchá (Czech Republic) and Sosnowiec (Poland) indicated by white asterisks (modified after Jureczka et al. 1995); B.(see below) Lithostratigraphic division of Pennsylvanian strata of Czech and Polish parts of the Upper Silesian Coal Basin after Dopita et al. (1997) with corresponding stratigraphical levels of both localities indicated by white asterisks. Abbreviations: Bolsov., Bolsovian; Duckman., Duckmantian (Prokop et al., 2012).



From a palaeogeographical point of view, it is similar to the coal basins of the European Variscides which form a belt stretching from the British Isles through Belgium to northern Germany and Polland. The basin is filled with continental and marine sediments from Lower and Upper Carboniferous and these sediments are divided into three main lithostratigraphical units - Hradecko-Kyjovické Formation, Ostrava Formation, Karviná Formation - in the Czech part, and Malinowice Beds. Paralic Series, Cracow Sandstone Series in Polish part (see Prokop et al., 2012).

The fossils studied in this thesis are preserved in sphero-sideritic concretions deposited by exploitation on spoilheaps in Sosnowiec-Klimontów. Originally, this material comes from Porąbka−Klimontów coal mine, which is located about about one kilometer from the temporary locality. According to macropalaeobotanical and palynological data, the nodules lithostrathigraphically belong to the Mudstone Series (lower part of the Załęże beds) of the Upper Carboniferous strata (Pacyna & Zdebska, 2012).

2.2 The formation of sideritic concretions

Sideritic conceretions containing plant and animal fossils have been found in Sosnowiec locality during the 1990s (Prokop et al., 2012).

Siderite is an authigenic mineral in sedimentary rocks, and forms concretions precipitating within the pore-spaces of sediments after deposition (Curtis et al., 1986; Mozley & Carothers, 1992). The formation of sideritic concretions necessarily requires the water environment (Baird et al., 1985, 1986). As a consequence of the accumulation of large volumes of organic material, the basin water formed reducing conditionss above a sediment base. Accumulated organic material sink to the bottom, where the concretions are quickly formed and protect the organic material from compaction through sediment loading (Pacyna & Zdebska, 2012). Sideritic concretions often reveals variation in chemical composition from the center to the outer edge. This variation is attributed to the changes in physical and chemical conditions in course of the concretion's growth starting from its center towards the rim, and is associated with the microbial processes within the sediments (Wilkinson et al., 2000).

The preservation in sideritic nodules has several advantages because it allows the preservation in three-dimensional form which is usefull especially for comparative morphology of delicate structures like insect wings (Pacyna & Zdebska 2012; Prokop et al., 2012).

2.3 Methods

Fossils presented in this paper were mostly observed under a stereomicroscope Leica MZ16 and Nikon SMZ 645, in dry state, but in some specimens a film layer of ethyl alcohol was applied. Patterns of the wing venation were drawn directly using a stereomicroscope with a camera lucida. Thereafter, drawings were readjusted with the photographs scale using of computer graphic software (Adobe Photoshop CS).

Photographs of the wings were took from dry specimens by digital camera Canon D550 with macro lenses MP-65 and EF-S 60 mm.

All material included in this thesis is housed in MP ISEA. In the following part we follow the wing venation nomenclature of Kukalová-Peck (1991). Abbreviations of wing veins: AA = anal anterior, AP = anal posterior, C = costa, CuA = cubitus anterior, CuP = cubitus posterior, MA = media anterior, MP = media posterior, RA = radius anterior, RP = radius posteriorů ScA = subcosta anterior, ScP = subcosta posterior. Systematics and divisions follow the conceptions of Riek (1976) and Sinitshenkova (2002).

In systematic part, we use the term “wing pad” for immature wings of Palaeodictyoptera in accordance with its meaning according to Nichols (1989).

3. SYSTEMATIC PART

Class Insecta Linnaeus, 1758
Infraclass Palaeoptera Martynov, 1923
Superorder Palaeodictyopteroidea Rohdendorf, 1961
Order Palaeodictyoptera Goldenberg, 1877
Superfamily Breyerioidea Handlirsch, 1904
Family ?Breyeriidae Handlirsch, 1904

Morphotype A

Diagnosis. Based on fore wing venation characters: all stems of main veins arising independently with prominent corrugation; cross veins not discernible; costal field of the wing broad and triangular in form of keel; concave ScP simple, weakly curved, presumably ending near the wing apex; RA and RP basally connected, RP diverging from RA at about a half of the wing-length, ending with two- or three branches; MA and MP basally fused, the point of divergence close to the wing base rather than division of RA and RP; convex MA simple, concave MP forked with two terminal branches; CuA and CuP arising from the stem of Cu; convex CuA simple, concave CuP ending with two or three branches; first anal vein deeply branched.

Referred material**. MP ISEA I-F/MP/1615/1abc/13** (consisting of three parts; a nearly complete larva with fragmentary preserved head, prothorax with large triangular winglets, meso- and metathorax bearing wing pads with discernible pattern of venation, abdomen with ten visible laterally enlarged segments, last segment of abdomen bearing a pair of cerci); **MP ISEA I-F/MP/1488/290/08** (imprint; partly preserved meso- and metathorax bearing posterolaterally directed wing pads with obvious venation, abdomen incomplete, first three segments not preserved, seven distal segments discernible and laterally enlarged**); MP ISEA I-F/MP/1576/326ab/10** (imprint and counter-imprint; meso- and metathoracic wing

pads with visible basal articulation and with relatively well-preserved venation pattern**); MP ISEA I-F/MP/1576/306ab/10** (imprint and counter-imprint; meso- and metathoracic wing pads with well-preserved venation pattern); **MP ISEA I-F/MP/1492/349ab/09** (imprint and counter-imprint; a well preserved mesothoracic immature wing and a part of tergum attached); **MP ISEA I-F/MP/1478/11ab/08** (imprint and counter-imprint; a well preserved prothoracic winglets, meso- and metathoracic wing pads with obvious venation pattern, abdomen partly preserved); **MP ISEA I-F/MP/1576/317ab/10** (imprint and counter-imprint; metathoracic wing pad with disrupted anterior margin and well preserved venation pattern); **MP ISEA J-F/MP/1616/1ab/13** (imprint and counter-imprint; thorax with prothoracic winglets of triangular shape, meso- and metathorax with posterolaterally directed wing pads, abdomen nearly complete); **MP ISEA I-F/MP/1492/355ab/09** (imprint and counter-imprint; partly disrupted thoracic segments bearing prothoracic winglets, mesothoracic wing pad with well preserved pattern of venation and metathoracic wing pad, abdomen with three segments discernable); **MP ISEA I-F/MP/1576/318ab/10** (imprint and counter-imprint; well preserved mesothoracic wing pad with partly preserved venation pattern and disrupted wing apex); **MP ISEA I-F/MP/1492/365ab/09** (imprint and counter-imprint; distorted thoracic segments with posterolaterally directed wing pads, abdomen with six visible proximal segments laterally enlarged, apical segments not preserved); **MP ISEA I-F/MP/1488/27ab/08** (imprint and counter-imprint; thorax with prothoracic winglets, meso- and metathoracic posterolaterally directed wing pads, abdomen with nine visible segments laterally enlarged); MP **ISEA I-F/MP/1576/305ab/10** (imprint and counter-imprint; disrupted thorax with prothoracic winglets, meso- and metathorax bearing posterolaterally directed wing pads, well preserved abdomen with ten abdominal segments visible).

Description.

Specimen MP ISEA I-F/MP/1615/1abc/13 (Figs. 16A, 18A)

Head: Small hypognathous head of round shape with compound eyes laterally preserved, mouthparts not visible - directed downwards.

Thorax: Prothorax rather short (estimated length about 2.9 mm), meso- and metathorax approximately equal in size (about 4.5 mm); prothorax bearing enlarged winglets of triangular shape with anterior margin basally incised close to the head; winglets well separated from prothorax with discernable basal muscle attachment; mesothorax bearing posterolaterally directed mesothoracic wing pads with prominent keel, venation with hyaline membrane; estimated length of the mesothoracic wing pad about 11 mm; width approximately 5.5 mm; costal area of the mesothoracic wing pad broad and triangular; the basal half of the anterior margin of the wing pad almost perpendicular to the body axis; attachment to the terga broad; concave ScP long and simple, weakly curved, parallel to RA; RA and RP basally connected, RP diverging from RA rather proximally at about a half of the wing-length; convex RA long and simple, ending at the apex of the wing pad; concave RP ending on the posterior wing margin with two main branches; MA and MP basally fused, MP separating from MA at about 1/3 the wing-length from the base; convex MA simple, distally strongly curved; concave MP forked into two branches reaching the posterior margin of the wing pad; stem of Cu divided into CuA and CuP at about 1/5 wing-length from the base; convex CuA simple, arched; concave CuP forked into two main branches; anal area of the wing pad rather broad, with poorly preserved anal vein; metathorax bearing metathoracic wing pads with narrower costal area; estimated length of the metathoracic wing pad about 9.4 mm; width approximately 4.6 mm; anterior margin of the hind wing pad partly covered by posterior margin of the mesothoracic wing pad; venation pattern similar to fore wing, but less visible; concave ScP simple, ending near the apex of the wing pad; RA and RP basally connected, RP diverging from RA at about a half of the wing-length, the point of divergence poorly preserved; convex RA simple, running parallel to ScP, ending at the apex of the wing; concave RP not discernible; M divided into MA and MP just proximally to the divergence-point of RA and RP; convex MA simple, distally strongly curved; concave MP forked into two branches reaching the posterior margin of the wing pad; CuA and CuP basally fused, CuP separating from CuA at about 1/4 of wing-length; convex

CuA simple, concave CuP deeply forked into two main branches; anal area rather broad with eight visible terminal offshoots preserved.

Abdomen: Ten abdominal segments slowly tapering towards the rear; length of abdominal segments approximately the same (about 2 mm); first segment partly covered by metathoracic wing pad; all segments bearing pointed posterolaterally directed heart-shaped structures with a prominent groove in the middle, directed to the apex of the structure; last abdominal segment bearing pair of basally stout cerci.

Specimen MP ISEA I-F/MP/1488/290/08 (Figs. 16B, 18B)

Thorax: Meso- and metathorax partly disrupted; mesothorax bearing posterolaterally directed wing pads with prominent keel, venation with hyaline membrane; costal area of the mesothoracic wing pad rather broad, basal part of anterior margin of the wing pad disrupted; concave ScP long, simple, weakly curved, ending in distal third of wing; RA and RP basally connected, RP diverging from RA at about 1/4 the wing-length from the base; convex RA simple, weakly curved, running parallel to ScP; RP dichotomously forked at about mid wing, reaching the posterior margin of the wing probably with two branches; MA not clearly discernible, concave MP terminally divided into two branches; CuA and CuP basally fused, CuP diverging from CuA at about 1/4 of the wing-length from the base; convex CuA simple, strongly curved; concave CuP terminally forked into two branches; anal area of the wing pad broad, with four offshoots of anal veins preserved; posterior margin of the wing pad not preserved. Metathorax length about 4.1 mm, bearing partly preserved metathoracic wing pad, venation with hyaline membrane; anterior margin of the wing pad and wing apex not preserved; estimated length of the metathoracic wing pad about 10 mm; convex RA straight and simple; concave RP simple, distally strongly curved, reaching the posterior margin close to the apex of the wing; MA and MP basally fused, the point of divergence MA and MP not discernible; convex MA simple, parallel to RP; concave MP deeply bifurcated at about mid wing, anterior and posterior branches both distally forked; CuA and CuP basally fused, CuP

diverging from CuA at about 1/4 of the wing-length from the base; convex CuA simple, arched; concave CuP divided into three branches; anal area of the hind wing broad, with seven anal veins preserved; convex 1A distally forked, 2A, 3A, 4A, 5A, 6A and 7A simple.

Abdomen: Slowly tapering towards the rear, with last seven abdominal segments visible; abdominal segments bearing posterolaterally directed heart-shaped structures with the prominent groove in the middle, parallel to the anterior margin of the lobe.

Specimen MP ISEA I-F/MP/1576/326ab/10 (Figs. 16C, 18C)

Partly preserved prothorax bearing enlarged winglets with several veins emerging from the base; mesothorax bearing posterolaterally directed mesothoracic wing pad of triangular shape, with prominent keel, originally with hyaline membrane; estimated length of the mesothoracic wing pad about 8.5 mm, width approximately 4.3 mm; costal area of the wing pad broad and triangular; the first half of anterior margin almost perpendicular to the body axis; concave ScP simple, weakly curved, ending close to the apex; RA and RP basally connected, RP diverging from RA at about a half of the wing-length; convex RA long and simple, running parallel to ScP, distally strongly curved, ending at the apex of the wing pad; concave RP pectinate ending on the posterior margin of the wing pad with three branches; stem of M not discernible; convex MA simple, strongly curved; the point of divergence between MA and MP not discernible; MP deeply forked into two branches reaching the posterior margin of the wing pad; CuA and CuP basally fused, CuA diverging from CuP at about 1/4 of the wing-length from the base; convex CuA simple, strongly curved; concave CuP pectinate ending on the posterior wing margin with three branches; anal area of the wing pad well developed, with four anal veins preserved; convex 1A deeply forked into two main branches, 2A, 3A, 4A simple; metathorax bearing posterolaterally directed wing pad; almost the entire margin of the metathoracic wing pad not preserved; estimated length of the metathoracic wing pad about 10 mm; concave ScP long and simple, parallel to RA; convex RA simple, running to the wing pad apex;

concave RP forked into two branches, one of them ending at the wing apex and the second reaching the posterior margin of the wing pad; stem of M not discernible; convex MA simple, distally strongly curved; concave MP diverging from MA; MP deeply forked into two branches; CuA and CuP basally fused, CuP diverging from CuA close to the base of the wing pad; convex CuA simple, strongly curved; concave CuP distally divided into two branches; anal area of the metathoracic pad rather broad, with four anal veins preserved; convex 1A pectinate reaching the posterior margin of the wing pad with five branches, 2A, 3A, 4A simple.

Specimen MP ISEA I-F/MP/1576/306ab/10 (Figs. 16D, 18D)

Mesothoracic wing pad of triangular shape, with prominent keel, originally with hyaline membrane; estimated length of the wing pad about 9 mm, width approximately 5 mm; costal area of the wing pad broad and triangular; concave ScP simple, weakly curved, running parallel to RA, ending in distal part of wing pad; RA and RP basally connected, point of divergence RP from RA not discernible; convex RA straight, simple, ending at the apex of the wing pad; concave RP divided into two branches, one of them reaching the apex and the second ending on the posterior margin of the wing pad; stem of M not discernible; convex MA simple, distally strongly curved; concave MP diverging from MA at about mid wing, ending on the posterior margin with two branches; CuA and CuP basally fused, CuA diverging from CuP at about 1/3 of the wing-length from the base; convex CuA simple, strongly curved, parallel to CuP; concave CuP forked into two branches; anal area of the wing pad broad, with four anal veins preserved; convex 1A deeply forked ending with two branches; 2A, 3A, 4A simple; anterior margin of the metathoracic wing pad not preserved; estimated length of the metathoracic wing pad about 7.8 mm, width approximately 4.5 mm; costal area probably rather narrower than in the mesothoracic one; concave ScP long and simple; convex RA simple, parallel to ScP, ending at the apex of the wing pad; RP diverging from RA at about mid wing; concave RP simple, distally strongly curved, reaching the posterior margin of the wing pad; MA and MP

basally fused, MP diverging from MA at about mid wing, the point of divergence not discernible; convex MA simple, strongly curved, more or less parallel to RP; concave MP deeply forked into two main branches; CuA and CuP basally fused, CuA diverging from CuP close to the base of the wing pad; convex CuA simple, arched; concave CuP reaching the posterior margin of the wing pad with two branches; anal area of the pad broader than in mesothoracic one, bearing five anal veins preserved; convex 1A pectinate ending on the posterior margin of the wing pad with four branches, 2A, 3A, 4A and 5A simple.

Specimen MP ISEA I-F/MP/1492/349ab/09 (Figs. 16E, 18E)

Mesothoracic wing pad with strongly curved costal margin, prominent keel and broad basal attachment to the tergum; posterior wing margin markedly reinforced, venation with hyaline membrane; estimated length of the mesothoracic wing pad about 11.6 mm, width approximately 6 mm; faint weakly convex CP, strongly curved, more or less parallel to the costal margin of the mesothoracic wing pad; concave ScP simple, weakly curved, more or less parallel to RA; RA and RP basally connected, RP diverging from RA at about a half of the wing-length; convex RA long and simple, reaching the apex of the wing pad; weakly concave RP pectinate ending on a posterior margin of the wing pad with three branches; stems of M divided into MA and MP rather distally at about 1/3 of the wing-length from the base; convex MA simple, strongly curved; concave MP deeply forked into two main branches reaching the posterior margin of the wing pad; CuA and CuP basally fused, CuA diverging from CuP close to the wing base; convex CuA simple, strongly curved; concave CuP distally forked into two main branches reaching the posterior margin of the wing pad at about a half of the wing-length; anal area of the wing pad rather broad, with two anal veins preserved, both basally connected by developing anal brace; convex 1A deeply forked into two branches; 2A simple.

Specimen MP ISEA I-F/MP/1478/11ab/08 (Figs. 16F, 18F)

Thorax: Prothorax bearing wing pads of triangular shape; meso- and metathoracic wing pads directed backwards; mesothoracic wing pad with prominent keel, venation originally with hyaline membrane; estimated length of the mesothoracic wing pad about 8.3 mm; costal area of the wing pad broad and triangular; concave ScP simple, weakly curved, ending probably close to the wing apex (apex and posterior margin of the wing pad disrupted); RA and RP basally connected, the point of divergence RA and RP at about mid wing; convex RA simple, parallel to ScP; concave or neutral RP incomplete; MA and MP basally fused, MP diverging from MA at about 1/3 of the wing-length from the base; convex MA simple, slightly curved; concave MP deeply forked into two main branches; CuA and CuP basally fused, CuP diverging from CuA approximately at about 1/5 of the wing-length from the base, the point of divergence not preserved; convex CuA simple, strongly curved to the posterior margin of the wing pad; concave CuP running parallel to CuA, distally forked into two main branches; anal area of the mesothoracic wing pad broad, with three anal veins preserved; convex 1A pectinate ending on the posterior margin of the wing pad with three branches, 2A and 3A simple; metathoracic wing pad with narrower costal field, originally with hyaline membrane; estimated length of the metathoracic wing pad about 7.8 mm; anterior margin and forepart of the wing pad covered by mesothoracic wing pad; concave ScP simple, running parallel to the anterior margin of the wing pad; convex RA simple, running parallel to ScP; RP forked into two branches reaching probably the wing pad apex; convex MA simple, distally strongly curved; concave MP divided into two main branches, each of them distally forked, MP reaching the posterior margin of the wing pad with four branches; convex CuA simple; CuP divided into two branches, posterior branch distally forked, CuP reaching the posterior margin of the wing pad with three branches; anal area of the pad rather broad, with five anal veins preserved; convex 1A pectinate ending on the posterior margin of the wing with four branches, 2A simple, 3A deeply forked, 4A and 5A simple.

Abdomen: Incomplete, with eight abdominal segments partly visible; length of abdominal segments approximately the same (about 1.6 mm); each abdominal

segment bearing distinctly enlarged posterolaterally directed heart-shaped structures as laterotergites.

Specimen MP ISEA I-F/MP/1576/317ab/10 (Figs. 17C, 19A)

Metathoracic wing pad with partly disrupted anterior margin; estimated length of the wing pad about 8 mm; convex RA simple, distally strongly curved, ending close to the wing pad apex; point of divergence RA and RP not discernible; RP divided into two main branches reaching the posterior margin of the wing pad; MA and MP basally fused, MP diverging from MA at about a half of the wing-length; convex MA simple, curved, parallel to MP; concave MP deeply forked into two branches; CuA and CuP basally fused, CuA diverging from CuP at about 1/4 of the wing-length from the base; convex CuA simple, strongly curved; concave CuP deeply forked ending with two main branches; anal area of the metathoracic wing pad broad, bearing three anal veins preserved; convex 1A arising from the developing anal brace, distally pectinate ending on the posterior margin with three branches; 2A and 3A simple.

Specimen MP ISEA J-F/MP/1616/1ab/13 (Figs. 17A, 19B)

Thorax: Prothorax a little bit shorter than meso- and metathorax (length about 2 mm), bearing enlarged winglets of triangular shape with several veins emerging from the base; Meso- and metathorax almost equal in length (about 3.7 mm); mesothorax bearing posterolaterally directed wing pads with prominent keel, originally with hyaline membrane; estimated length of mesothoracic wing pad about 9 mm, width approximately 5 mm; first half of the anterior margin of the mesothoracic wing pad nearly perpendicular to the body axis; costal area of the wing pad broad and triangular; concave ScP simple, weakly curved, running parallel to RA; RA and RP basally connected, RP diverging from RA at about 1/3 of the wing-length from the base; convex RA simple, ending at the apex of the wing pad; concave RP deeply forked into two branches; MA and MP basally fused, MP diverging from MA probably closer to the base than in RA and RP, but the point of divergence not discernible; convex MA simple, distally strongly

curved; concave MP reaching the posterior margin of the wing pad with two main branches; CuA and CuP basally fused, CuP diverging from CuA close to the wing base; convex CuA simple, strongly curved; concave CuP deeply forked with two branches reaching the posterior margin; anal area of the mesothoracic wing pad rather broad, with two anal veins preserved; convex 1A pectinate ending on the posterior margin with three branches, 2A simple; metathorax bearing broadly attached posterolaterally directed wing pads, originally with hyaline membrane; estimated length of the metathoracic wing pad about 7.5 mm; anterior margin of the wing pad covered by mesothoracic wing pad; concave ScP weakly preserved, long and simple, running more or less parallel to RA; RA and RP basally connected, RP diverging from RA at about a half of the wing-length; convex RA long and simple, ending probably at the disrupted apex of the wing pad; concave RP pectinate ending on the posterior margin of the wing pad with three branches; MA and MP basally fused; the point of divergence of MA and MP not discernible; convex MA simple, strongly curved; concave MP running parallel to MA, pectinate ending with three terminal branches; CuA and CuP basally fused, CuP diverging from CuA close to the wing base; convex CuA simple;; concave CuP simple; anal area of the mesothoracic wing pad broad, with two anal veins preserved; convex 1A forked into two branches ending on the posterior margin of the wing pad; second anal vein 2A pectinate ending on the posterior margin of the wing pad with six visible branches;

Abdomen: Relatively slender abdomen showing median ridge; abdominal segments not recognizable; abdomen slowly tapering towards the rear; last abdominal segment not preserved.

Specimen MP ISEA I-F/MP/1492/355ab/09 (Figs. 17D, 19C)

Thorax: Prothorax shorter than meso- and metathorax, bearing enlarged prothoracic winglets of triangular shape with several veins emerging from the base; mesothorax bearing mesothoracic wing pad with prominent keel, originally with hyaline membrane; estimated length of the mesothoracic wing pad about 10 mm, width approximately 5.1 mm; wing attachment to the tergum rather broad;

costal field of the mesothoracic wing pad broad of triangular shape; vein CP simple, running more or less parallel to the anterior margin of the wing pad; concave ScP simple, running parallel to RA; RA and RP basally connected, RP diverging from RA at about a half of the wing-length; convex RA long, simple, ending at the wing pad apex; concave RP divided into two branches at about a half of its length; convex MA simple, distally curved, reaching the posterior wing margin; concave MP deeply forked into two main branches; CuA and CuP basally fused, CuP diverging from CuA close to the base of the wing pad; convex CuA simple and strongly curved; concave CuP divided into two branches; anal area of the mesothoracic wing pad rather broad, with convex 1A simple; metathorax bearing posterolaterally directed wing pad with narrower costal area; concave ScP simple, parallel to RA; RA and RP basally connected, RP diverging from RA at about 1/4 of the wing-length from the base; convex RA simple, distally strongly curved, ending at the apex of the wing pad, concave RP probably simple; concave MP simple; convex CuA simple, distally curved; concave CuP diverging from CuA at about a half of the wing-length from the base; CuP forked into two main branches reaching the posterior margin of the wing pad; anal area of the metathoracic wing pad broad, with two anal veins discernible.

Abdomen: First three abdominal segments partly visible, size of each abdominal segment approximately the same (about 1.6 mm).

Specimen MP ISEA I-F/MP/1576/318ab/10 (Figs. 17E, 19D)

Mesothoracic wing pad of triangular shape, with prominent keel, originally with hyaline membrane; estimated length of the mesothoracic wing pad about 8 mm, width approximately 4.5 mm; costal area of the wing pad broad and triangular; faint vein CP simple, running parallel to the anterior margin of the wing pad; concave ScP simple, weakly curved, running parallel to RA, ending probably near the disrupted apex of the wing pad; RA and RP basally connected, RP diverging from RA close to the mid wing; convex RA simple, running to the apex of the wing pad; concave RP not well discernible, probably deeply forked into two branches reaching the posterior margin of the wing pad; MA and MP basally

fused, MP diverging from MA at about 1/3 of the wing-length from the base; convex MA simple, strongly curved; concave MP simple, running parallel to MA; CuA and CuP basally fused, CuP diverging from CuA at about 1/4 of the wing-length from the base; convex CuA simple, strongly curved; concave CuP forked into two branches; anal area of the wing pad rather broad, with three anal veins preserved; convex 1A simple, strongly curved; pectinate 2A ending on the posterior margin with four branches; 3A simple.

Specimen MP ISEA I-F/MP/1492/365ab/09 (Figs. 17B, 19E)

Thorax: Prothorax detached, bearing fragment of enlarged winglet, meso- and metathoracic segments fragmentary bearing posterolaterally directed wing pads; mesothoracic wing pad with prominent keel, originally with hyaline membrane, pattern of venation of main longitudinal veins faintly recognizable; attachment of the wing pad to the tergum broad, reinforced in anterior part as sclerite; estimated length of the mesothoracic wing pad about 8 mm; concave ScP simple, weakly curved; RA and RP basally connected, RP diverging from RA at about 2/5 of the wing-length from the base; convex RA simple, parallel to ScP, running to the wing pad apex; concave RP forked into two branches at about 1/2 of its length; MA and MP basally fused, MP diverging from MA at about the same level as RA and RP, the point of divergence not discernible; convex MA simple, distally strongly curved; concave MP distally forked into two branches reaching the posterior margin of the wing pad; CuA and CuP basally fused; convex CuA simple, distally strongly curved; concave CuP strongly curved with marked trichotomy; anal field of the mesothoracic wing pad rather broad, with two simple anal veins preserved; metathorax bearing metathoracic wing pad also clearly attached and reinforced in anterior part of the base; pattern of venation less obvious than in mesothoracic one; convex CuA simple, distally curved; concave CuP divided into two branches, anterior branch running close to CuA; anal area of the wing pad broad, with five simple anal veins preserved.

Abdomen: Slowly tapering towards the rear, with first seven abdominal segments preserved; length of abdominal segments approximately the same (?length about

1.6 mm); posterior margin of each segment weakly concave; all abdominal segments bearing pointed, posterolaterally directed heart-shaped structures with the groove in the middle, parallel to the anterior margin of the lobe; anterior margin of each lobe strongly convex.

Specimen MP ISEA I-F/MP/1488/27ab/08 (Fig. 20A)

Prothorax rather smaller than mesothorax and metathorax, bearing small prothoracic winglets; mesothorax and metathorax approximately equal in length, mesothorax with mesothoracic wing pads of nearly triangular shape and only partly discernible pattern of venation; mesothoracic wing pad with prominent keel, originally with hyaline membrane, cross-veins not developed; broad costal area; concave ScP simple, running parallel to RA; convex RA simple, division of RA and RP not dicernable; convex MA and convex CuA visible; anal area of the fore wing rather broad, four anal veins preserved; metathorax bearing rather smaller metathoracic wing pad with narrower costal area; concave ScP weakly curved, reaching the wing pad apex; the point of divergence of RA and RP not visible; convex RA simple, parallel to ScP, concave RP simple; convex MA simple, weakly curved, reaching the posterior margin of the wing pad; convex CuA simple; abdomen slowly tapering towards the rear, with median keel and with nine discernible abdominal segments laterally enlarged, bearing posterolaterally directed heart-shaped structures with strongly convex anterior margin; last abdominal segment bearing a pair of cerci.

Specimen MP ISEA I-F/MP/1576/305ab/10 (Fig. 20B)

Prothorax bearing partly preserved small prothoracic winglets of triangular shape; mesothorax bearing posterolaterally directed mesothoracic wing pad with prominent keel, originally with hyaline membrane; estimated length of the mesothoracic wing pad 8.6 mm; venation pattern not well preserved; costal area of the pad broad and triangular; first half of the anterior margin of the pad perpendicular to the body axis; concave ScP simple; RA and RP basally fused, RP diverging from RA at about 1/3 of the pad- length from the base; convex RA

simple, parallel to ScP, reaching the wing apex; concave RP simple; metathorax with metathoracic wing pad, rather smaller than the mesothoracic one; anterior margin of the pad disrupted; convex CuA and concave CuP, forked into two branches visible; anal area of the wing pad with two anal veins preserved; well preserved abdomen with ten abdominal segments visible; length of the second abdominal segment approximately 2.7 mm; abdomen slowly tapering towards the rear, length of abdominal segments approximately the same; abdominal segments bearing posterolaterally directed, pointed lateral projections.

Explanation of figures:

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Figure 16. Drawings of immature wings of Morphotype A. - A**. MP ISEA I-F/MP/1615/1abc/13**; B. **MP ISEA I-F/MP/1488/290/08**; C. **MP ISEA I-F/MP/1576/326ab/10**; D. **MP ISEA I-F/MP/1576/306ab/10**; E. **MP ISEA I-F/MP/1492/349ab/09**; F**. MP ISEA I-F/MP/1478/11ab/08**. Vein symbols are abbreviated as follows: CP, Costa posterior; ScP, Subcosta posterior; RA/RP, Radius anterior/posterior; MP, Media posterior; CuA/CuP, Cubitus anterior/posterior; A, anal area.

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Figure 17. Drawings of immature wings of Morphotype A (A-E) and Morphotype B (F). - A. **MP ISEA J-F/MP/1616/1ab/13**; B. **MP ISEA I-F/MP/1492/365ab/09**; C. **. MP ISEA I-F/MP/1576/317ab/10**; D. **MP ISEA I-F/MP/1492/355ab/09**; E. **MP ISEA I-F/MP/1576/318ab/10**; F. **MP ISEA J-F/MP/1594/1ab/11**. Vein symbols are abbreviated as follows: ScP, Subcosta posterior; RA/RP, Radius anterior/posterior; MP, Media posterior; CuA/CuP, Cubitus anterior/posterior; A, anal area

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Figure 18. Photographs of immature wings of Morphotype A. - A. **MP ISEA I-F/MP/1615/1abc/13**; B. **MP ISEA I-F/MP/1488/290/08**; C. **MP ISEA I-F/MP/1576/326ab/10**; D. **MP ISEA I-F/MP/1576/306ab/10**; E. **MP ISEA I-F/MP/1492/349ab/09**; F. **MP ISEA I-F/MP/1478/11ab/08**. Vein symbols are abbreviated as follows: ScP, Subcosta posterior; RA/RP, Radius anterior/posterior; MP, Media posterior; CuA/CuP, Cubitus anterior/posterior; A, anal area

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Figure 19. Photographs of immature wings of Morphotype A (A-E) and B (F). - A**. MP ISEA I-F/MP/1576/317ab/10**; B. **MP ISEA J-F/MP/1616/1ab/13**; C. **MP ISEA I-F/MP/1492/355ab/09**; D. **MP ISEA I-F/MP/1576/318ab/10**; E. **MP ISEA I-F/MP/1492/365ab/09**; F. **MP ISEA J-F/MP/1594/1ab/11**. Vein symbols are abbreviated as follows: CP, Costa posterior; ScP, Subcosta posterior; RA/RP, Radius anterior/posterior; MP, Media posterior; CuA/CuP, Cubitus anterior/posterior; A, anal area

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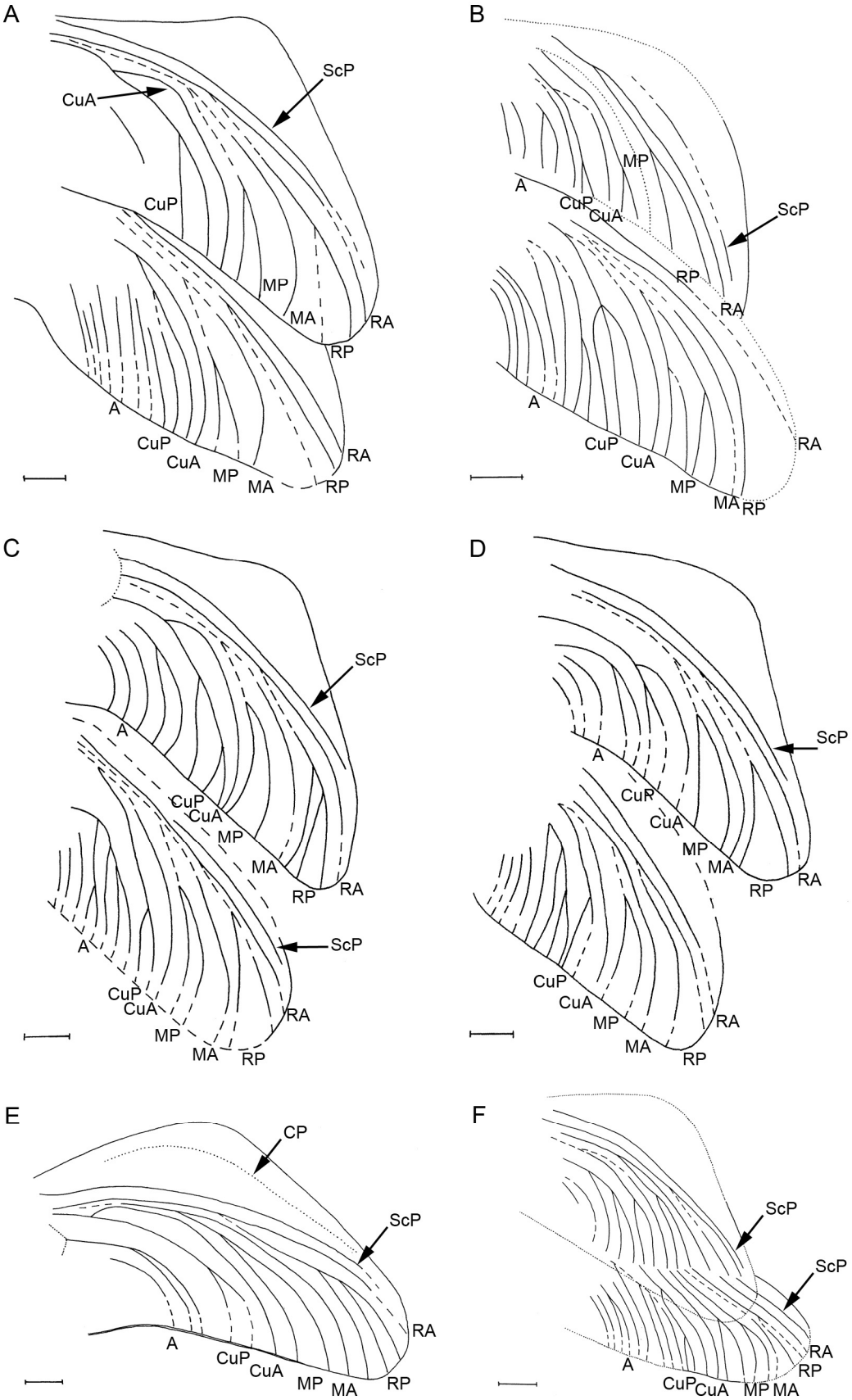
Figure 20. Photographs of immature wings of Morphotype A. - A. **MP ISEA I-F/MP/1488/27ab/08**; B. **MP ISEA I-F/MP/1576/305ab/10**


A
ScP
CuA
CuP
MP
MA
RA
RP
A
CuP
CuA
MP
MA
RP
RA
B
MP
A
CuP
CuA
ScP
RP
RA
A
CuP
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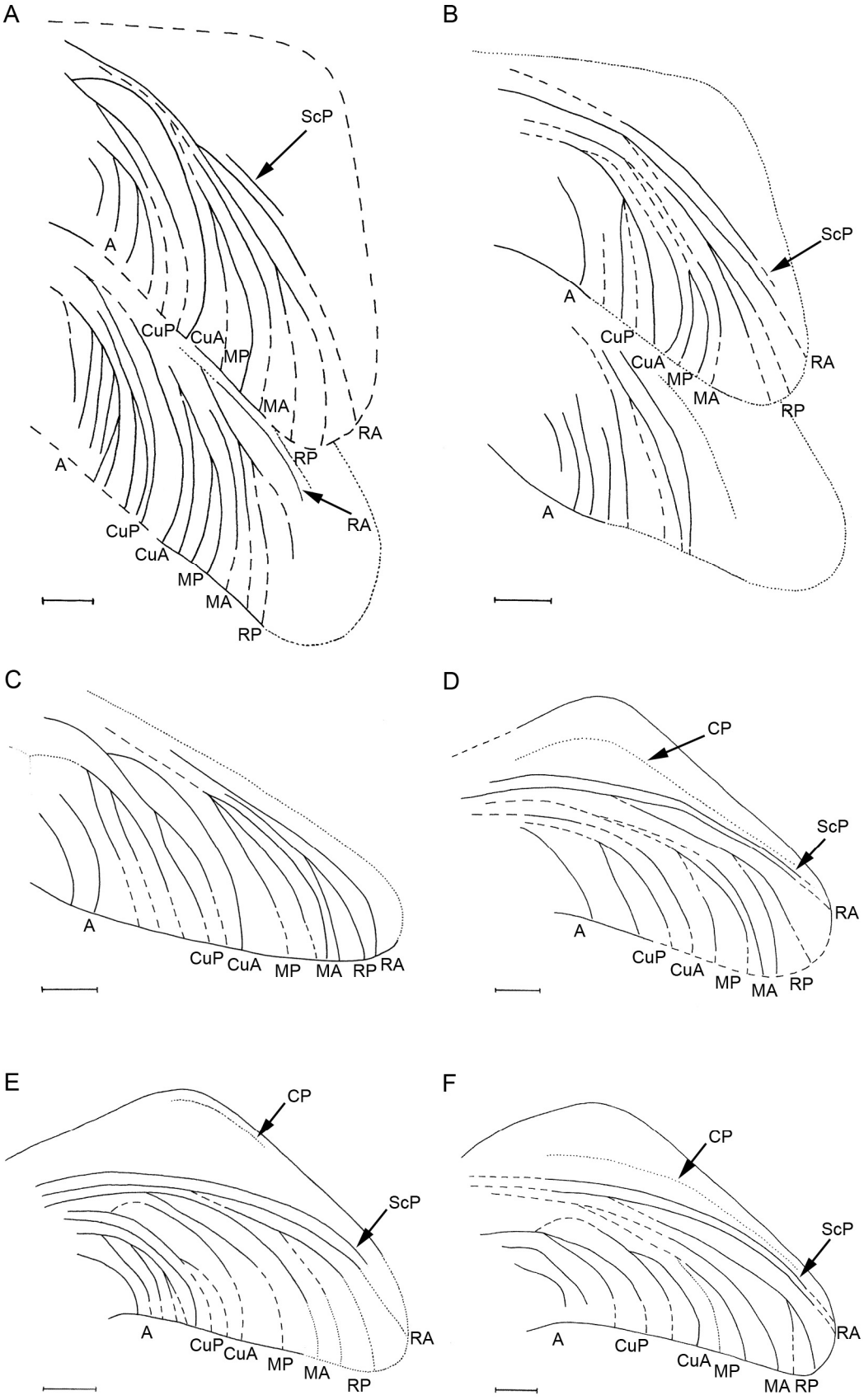
A
ScP
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CuP
CuA
MP
MA
RA
RP
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CuP
CuA
MP
MA
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RA
B
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CuA
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RP
A
C
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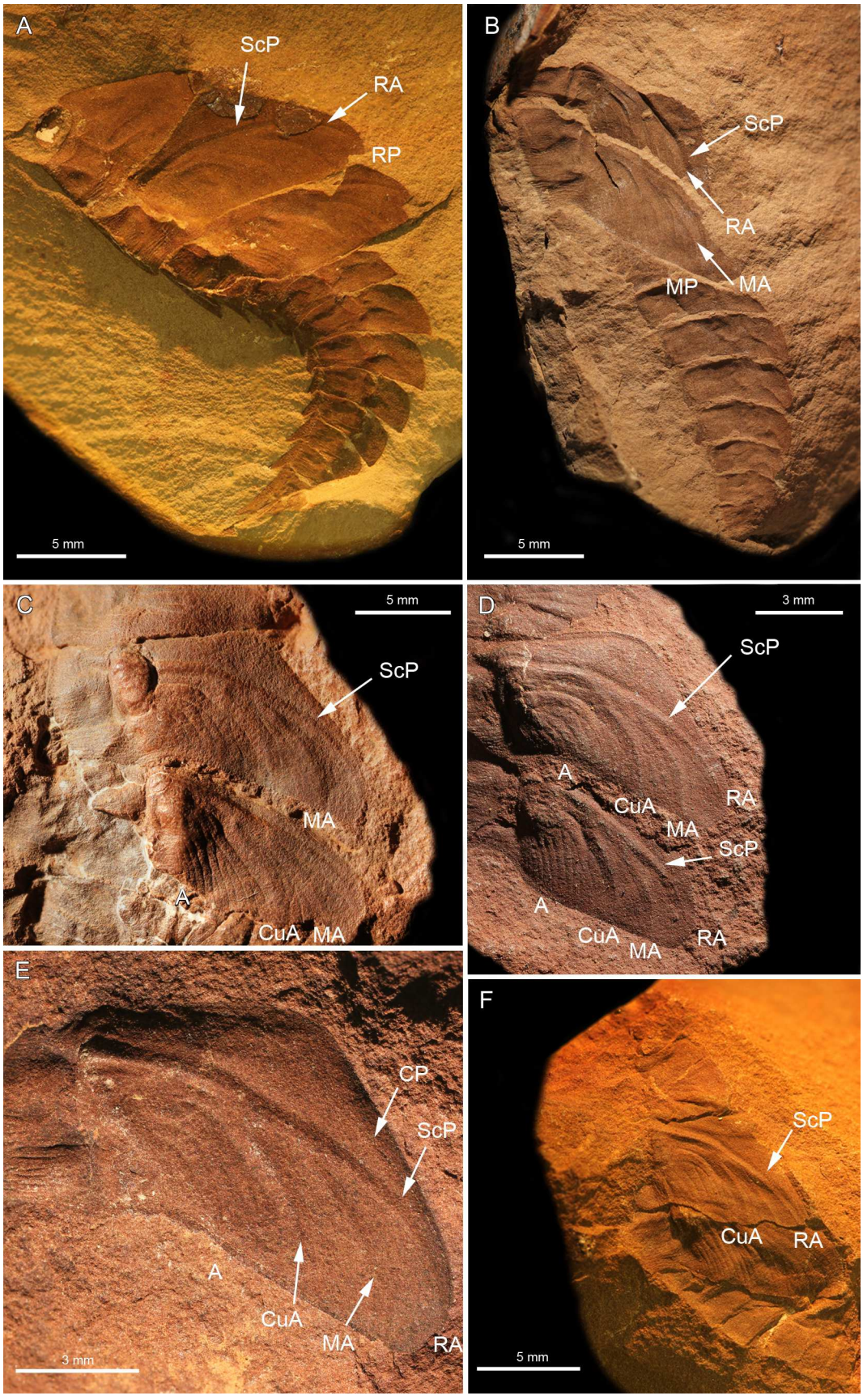
A
ScP
RA
RP
5 mm
B
ScP
RA
MP
MA
5 mm
C
5 mm
ScP
MA
A
CuA
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D
3 mm
ScP
A
CuA
RA
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CP
ScP
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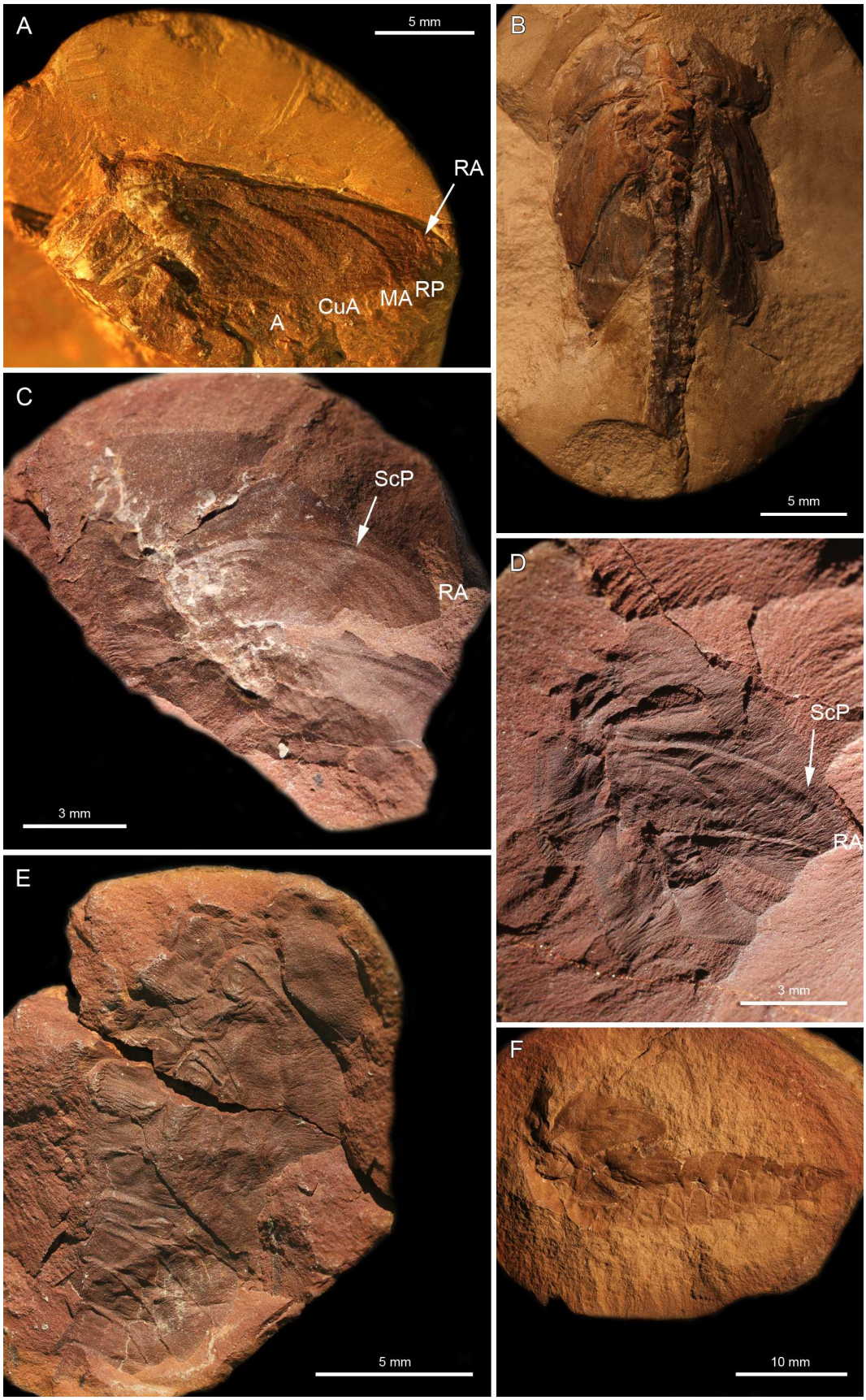
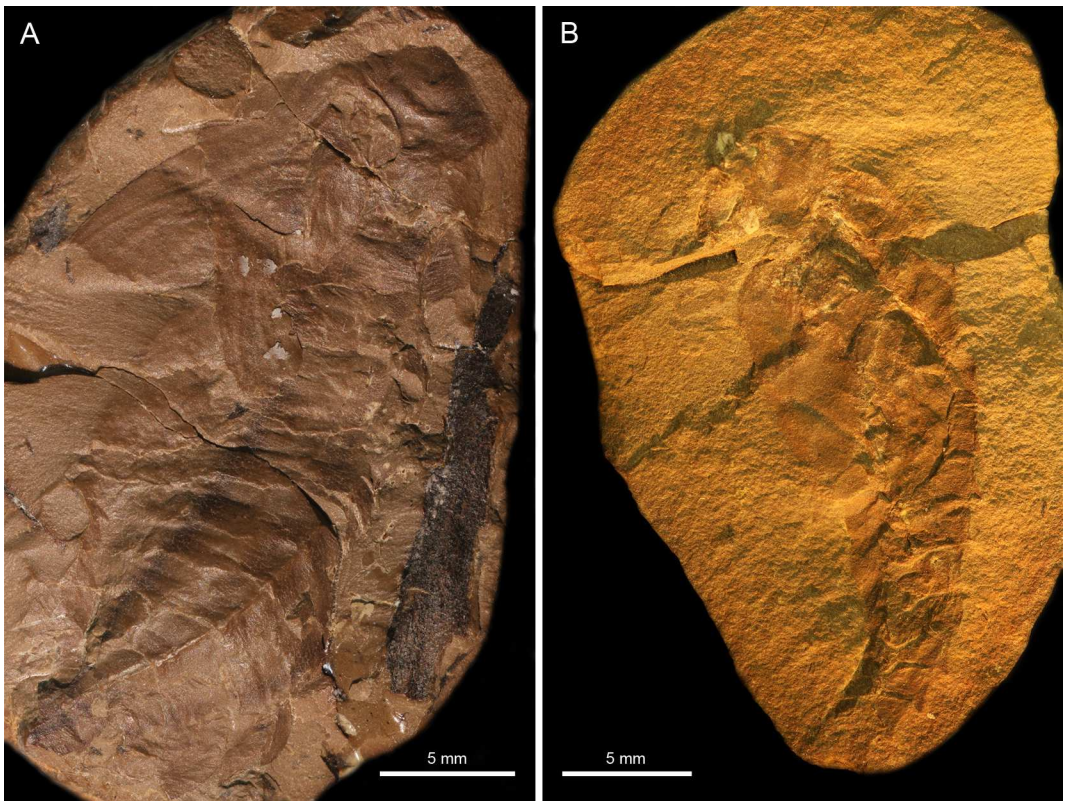
MA
RA
3 mm
F
ScP
CuA
RA
5 mm


A
5 mm
RA
RP
MA
CuA
A
B
5 mm
C
ScP
RA
3 mm
D
ScP
RA
3 mm
E
5 mm
F
10 mm


A
5 mm
B
5 mm

DISCUSSION

Morphotype A display the combination of the following venation characters supporting its placement to order Palaeodictyoptera: (1) wings in outstretched position protruding laterally; (2) presence of broadly attached prothoracic lobes of triangular shape; and (3) presence of all main longitudinal veins distinctly corrugated.

Morphotype A has fore- and hind wings similar in size and venation pattern although there are certain small differences in broadness of anal area. Fore wings are of nearly triangular shape due to prominent anterior keel indicating early larval instar. It is possible that the prominent keel had protective function because it is significantly developed in fore wings while in hind wings is not so prominent. Mesothoracic wing pads as well as metathoracic wing pads are broadly attached to their respective thoracic segments. All main longitudinal veins preserved are present with prominent corrugation as follow: RA, MA and CuA convex, ScP, RP, MP and CuP concave. In several specimens, the faint vein CP is recognizable remote from anterior margin of the wing pad (e.g figs. 20E, 21C, 21D), which become fused in later instars with CA to support and reinforced the anterior margin of the wing (Kukalová-Peck, 1978). Convex vein ScA commonly present in adult wings is not discernable on our fossils probably due to preservation. ScP is simple, extending almost to the apex of the wing pad. RA and RP are basally connected, with RP diverging from RA at about a half of the wing-length. RA is always simple, whilst RP is concave or neutral distally divided into two or three branches. Stem of M is divided into MA and MP. MA is simple in all cases, while MP is either simple or distally forked into two branches. CuA and CuP are basally fused, with CuP diverging from CuA close to the base of the wing pad. CuA is always simple, strongly curved to the posterior wing margin, CuP is two- or three branched. The anal area in fore wings is rather reduced, with several anal veins preserved, first anal vein usually ending with terminal branches. Anal area in hind wings is more developed than in fore wings, suggesting that hind wings could be probably basally broader than fore wings in adults.

Differences in the number of terminal branches of the main longitudinal veins between fore- and hind wings in various specimens of Morphotype A are probably due to infraspecific variability. For example, Carpenter & Richardson (1971) described the palaeodictyopterous nymph *Lycodemas adolescens* Carpenter & Richardson, 1971 and attributed it to the family Lycocercidae despite the fact that MP in *Lycodemas* was with less developed branches than it is proposed for the family Lycocercidae (see Carpenter, 1992).

Until now, the classification of the extinct order Palaeodictyoptera is still incompletely understood, even after the exhaustive revision of the species, well known from Commentry in France (Kukalová-Peck, 1969a, 1969b, 1970).

According to the simplified key of Riek (1976) there are six major superfamilies as follows: Breyeroidea, Calvertielloidea, Dictyoneuroidea, Dictyoptiloidea (= Eugereonoidea *sensu* Sinitshenkova, 2002), Homoiopteroidea and Spilapteroidea. These superfamilies can be mainly separated by the wing venation characters as follow: development of the archedictyon or pattern of cross veins, combined with the branching of main veins: MA, MP, CuA and CuP.

The new phylogeny and system of the superorder Dictyoneurida Handlirsch, 1906 (= Eupalaeodictyoptera *sensu* Riek, 1976) have been proposed by Sinitshenkova (2002b) which is partly based on the work of Riek (1976). Although this system uses cladistic terminology, it is not based on the cladistic methods (Prokop & Nel, 2004). Main division of the superorder Dictyoneurida into two groups is primarily based on wing characters. The group Dictyoneurina contains all members with basally broad wings, while the group Frankenholziina contains members with basally narrow wings (Sinitshenkova, 2002b).

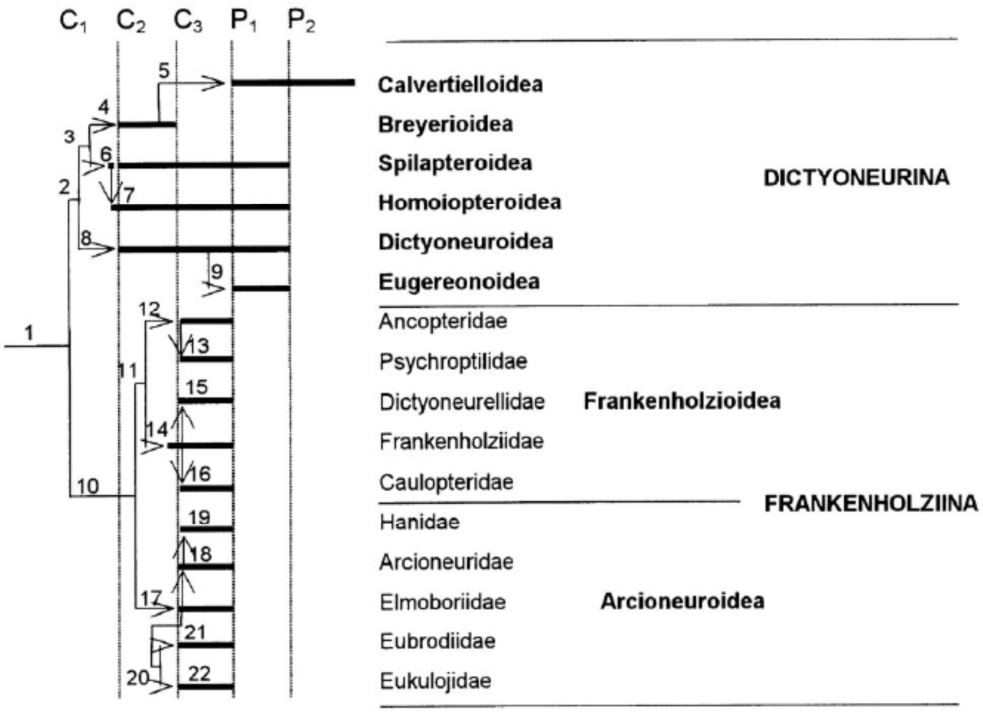


Figure 21. ´Phylogenetic´ system of the order Dictyoneurida. Time periods are abbreviated as follows: C1, C2, C3 – Early (Lower), Middle and Late (Upper) Carboniferous, P1, P2 – Early (Lower) and Late (Upper) Permian. Three righthand columns are names of families, superfamilies and suborders, respectively (Sinitshenkova, 2002b).

All six superfamilies previously proposed by Riek (1976) belongs to the group Dictyoneurina, thus their wings are broadly attached to the tergum. Eugereonoidea Handlirsch, 1906 (= Dictyoptiloidea *sensu* Riek, 1976) is the largest superfamily comprising 11 families as follows: Archamegaptilidae Handlirsch, 1919, Eugereonidae Handlirsch, 1906, Graphiptilidae Handlirsch, 1906, Jongmansiidae Laurentiaux, 1949, Lithomanteidae Handlirsch, 1906, Lycocercidae Handlirsch, 1906, Megaptilidae Handlirsch, 1906, Polycreagridae Handlirsch, 1906, Protagriidae Handlirsch, 1906, Synarmogidae Handlirsch, 1910, Tchirkovaeidae Sinitshenkova, 1979. Wings of Eugereonoidea are characterized by length 2.5 times of its width. Superfamily Dictyoneuroidea contains 3 families as follows: Dictyoneuridae Handlirsch, 1906, Peromapteridae Handlirsch, 1906 (synonymized with Eugereonidae by Carpenter (1992)) and Saarlandidae Guthörl, 1930. Members of Dictyoneuroidea are similar to Eugereonoidea, but differ in

wing length 3.5 times of its width. Superfamily Breyerioidea include three families as follows: Breyeriidae Handlirsch, 1906, Stobbsiidae Handlirsch, 1908 and Cryptoveniidae Bolton, 1912 (Sinitshenkova, 2002b).

Riek (1976) proposed four superfamilies (Breyeroidea, Calvertielloidea, Dictyoneuroidea, Dictyoptiloidea) in which both veins MA and CuA are unbranched as present in Morphotype A. Two remaining superfamilies Homoiopteroidea and Spilapteroidea can be excluded having CuA distinctly multi branched.

According to Riek (1976) and Sinitshenkova (2002b), in Dictyoneuroidea and Dictyoptiloidea ScP is extending almost to the wing apex which is character shared by Morphotype A, while in Breyerioidea and Calvertielloidea ScP is distinctly shorter, scarcely longer than a half of the wing-length, usually connected with RA. However, there have been recently described breyeriids as *Breyeria harlemensis* Brauckmann & Gröning, 1996 from Upper Carboniferous of Germany with ScP ending on the anterior margin near the apex of the wing (Brauckmann & Gröning, 1996). For this reason, we consider this character as variable (see figs. 23, 24 below).

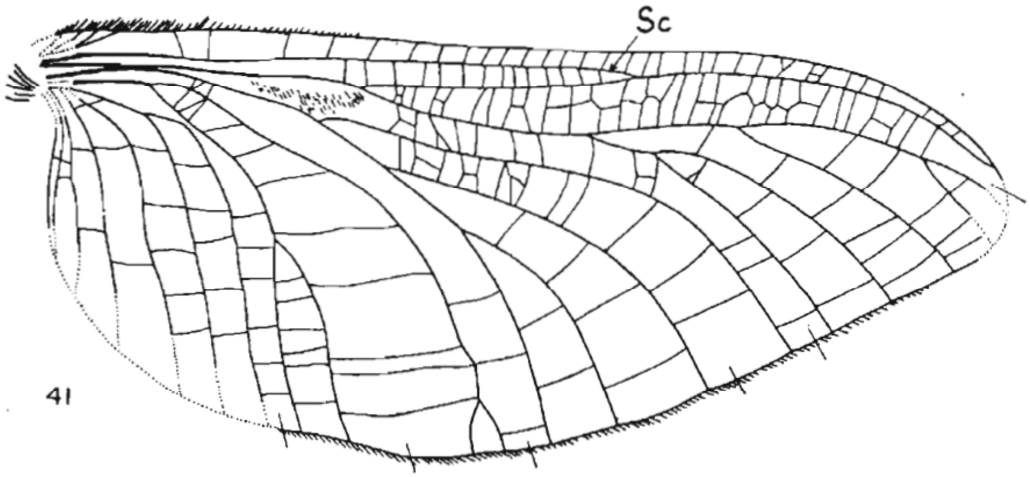


Figure 22. *Breyeria boulei* (Meunier), hind wing, holotype (Kukalová, 1969b).

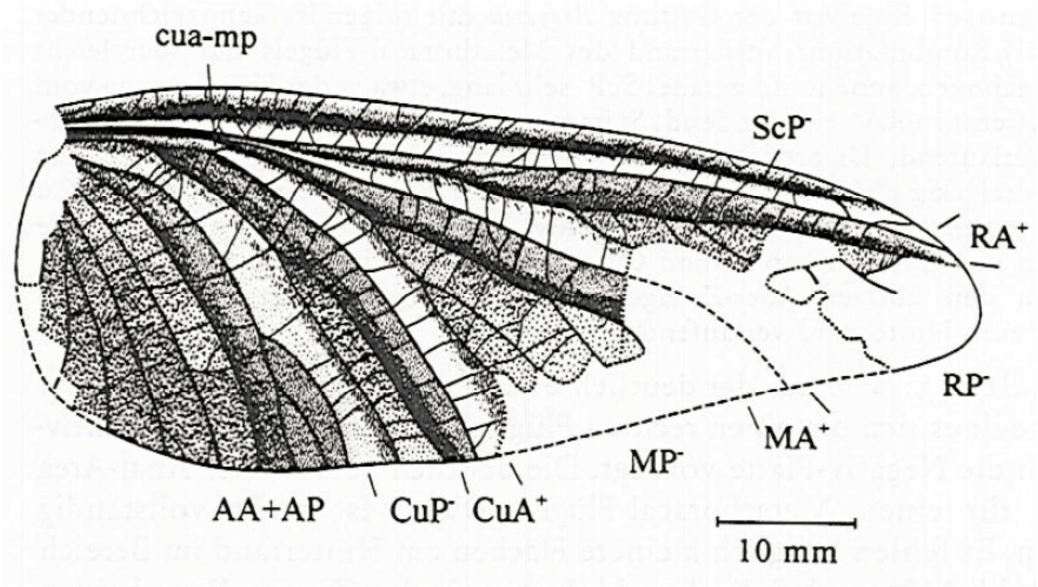


Figure 23. *Breyeria harlemensis* n. sp., hind wing, holotype, Westfal A, South Limburg basin, The Netherlands (Brauckmann & Gröning, 1996).

In Breyerioidea, both veins CuP and MP are branched, while only MP is branched in Calvertielloidea. CuP is distinctly basally separated from the stem of M in Breyerioidea, whereas in latter superfamily CuA appears to arise from the stem of M (Riek, 1976).

It follows from the above that Morphotype A is most likely attributable to the superfamilies Breyerioidea, Dictyoneuroidea or Dictyoptiloidea (= Eugereonoidea *sensu* Sinitshenkova, 2002b).

Superfamily Dictyoneuroidea is characterized by presence of well developed dense pattern of cross veins so called archedictyon, unlike in Morphotype A. However, it is possible that some changes take place during the wing development when the wings gradually elongate and become more straightened (Kukalová-Peck, 1991). Thus, archedictyon may be developed later, as it is proposed in Sinitshenkova (1979) and confirmed on paoliids by Prokop et al. (2012). On the other hand, superfamily Dictyoptiloidea is based on reduction of archedictyon, which corresponds with Morphotype A. Cross veins in adult breyerioids are very fine and irregularly arranged supporting their lack in immature stages as present in Morphotype A. Hind wings in members of Breyerioidea are markedly broader

than fore wings, which support the placement of Morphotype A within this group (Carpenter, 1992). Prokop et al. (2013) demonstrated differences between fore- and hind wings of older instars tentatively attributed to breyeriids, too.

Therefore, we proposed the attribution of Morphotype A to the superfamily Breyerioidea consisting of three families Breyeriidae, Stobbsiidae and Cryptoveniidae.

In Breyeriidae, veins MP, CuA and CuP are strongly curved towards the posterior margin of the wing (Kukalová-Peck, 1969a, 1969b, 1970) and members of Breyeriidae are known from a short interval from the Bashkirian to Gzhelian in Upper Carboniferous deposits in western and central Europe (Belgium, Czech Republic, England, France, Germany and The Netherlands) and USA (Tennessee)(Carpenter, 1992; Brauckmann & Gröning, 1996) and thus attribution of Morphotype A into this family seems likely.

We propose to attribute the Morphotype A to the family Breyeriidae which is defined by following characters: (1) fore wing broad; (2) costal margin of the wing strongly curved; (3) ScP ending before the wing apex; (4) basally connected RA and RP very close to the stem of M; (5) RP with five or six branches distinctly separated; (6) CuA unbranched; (7) CuP usually forked; (8) hind wing broader than fore wing; (9) fore and hind wing equal in length (Kukalová, 1969a; 1969b; 1970; Carpenter, 1992; Prokop & Ren, 2007). Character (5) is not corresponding with Morphotype A in which RP is two- or three branched (see figs. 20 A-F, 21 A-E). However, this minor difference may be due to the fact that wings in Morphotype A are immature, and wing venation is only partly developed, thus several other veins may emerge during the development (Handlirsch, 1906; Carpenter, 1948; Carpenter & Richardson, 1971; Kukalová-Peck & Peck, 1976).

Surpricely to date only few palaeodictyopterous nymphs have been described. *Rochdalia parkeri* Woodward, 1913 was originally described as branchiopod crustacean, and later re-described by Rolfe (1967) who stated that *Rochdalia* is actually an insect nymph, and tentatively attributed it to the family Breyeriidae. Wootton (1972) supported the attribution of *Rochdalia* to the order

Palaeodictyoptera, but he concluded that it is not possible to assign genus *Rochdalia* to any palaeodictyopterous family due to lack of differentiating characters. The wing venation in *Rochdalia* is poorly preserved with only few characters as ScP extending to the wing apex and discernible alternation of convexities and concavities of RA, partly RP and MA. Wootton (1972) established the new genus *Idoptilus* based on *Idoptilus onisciformis* Wootton, 1972 from Upper Carboniferous of England. The wing venation of *Idoptilus* is well preserved in comparison to *Rochdalia* and strongly resembles the pattern present in Morphotype A. *Idoptilus* differs mainly by the RP pectinate ending with four branches and MP ending with five branches unlike in Morphotype A.

Another species of the same genus as *Idoptilus peachii* (Woodward, 1887b) was first described as a cockroach nymph by Woodward, and later revised and considered as onisciform nymph of Palaeodictyoptera (Ross, 2010). However, the venation pattern in *Idoptilus peachii* (Woodward, 1887b) is very faint. Only four main longitudinal veins are discernible as RA, MA and CuA, each of them diverging to the posterior wing margin. Due to poor preservation of the venation pattern, there are no reliable characters distinguishing *Idoptilus peachii* (Woodward, 1887b) from *Idoptilus onisciformis* Wootton, 1972.

Carpenter (1992) considered palaeodictyopteran nymphs known from the British Carboniferous Coal Measures such as *Rochdalia parkeri* Woodward, 1913, *Idoptilus onisciformis* Wotton, 1972 with uncertain ordinal assignment.

However, all these nymphs having the prothoracic lobes of triangular shape, wings are in outstretched position with prominent keel in fore wings, and the wing venation with main longitudinal veins typically corrugated. Thus we have no doubt about their palaeodictyopterous affinity contra Carpenter (1992).

Idoptilus resembles the family Breyeriidae in having hind wing basally broader than fore wing, but equal in length, but its assignment to the certain family seems to be impossible due to lack of defining characters (Wootton, 1972).

Other palaeodictyopterous nymphs have been described from Upper Carboniferous of Illinois and Siberia (see Carpenter & Richardson, 1971; Sinitshenkova, 1979). But these nymphs are strikingly different from genera

Rochdalia, *Idoptilus* and from Morphotype A, because they are not onisciform larval type (Ross, 2010). They have been attributed to the families Lycocercidae Handlirsch, 1906 (Carpenter & Richardson, 1971) and Tchirkovaeidae Sinitshenkova, 1979 (Sinitshenkova, 1979).

Superfamily Homoiopteroidea Handlirsch, 1906
Family ?Homoiopteridae Handlirsch, 1906

Morphotype B

Diagnosis. Based on fore wing venation characters; all main longitudinal veins present with prominent corrugation; costal field of the wing broad and triangular in form of keel; concave ScP simple, weakly curved, ending at the apex of the wing; RA and RP basally connected, RP diverging from RA at about a half of the wing-length, divided into two branches; MA simple, strongly curved; MP forked with two terminal branches; CuA and CuP arise from the stem of Cu; CuA divided into two branches, CuP divided into two branches.

Reffered material.
MP ISEA J-F/MP/1594/1ab/11 (imprint and counter-imprint; partly disrupted thorax, meso- and metathorax bearing posterolaterally directed wing pads with recognizable pattern of venation, abdomen with ten visible segments laterally enlarged, last abdominal segment bearing a pair of cerci).

Description.
Specimen MP ISEA J-F/MP/1594/1ab/11 (Figs. 17F, 19F)
Thorax: Prothorax bearing small prothoracic winglets; mesothorax with posterolaterally directed wing pads of triangular shape, with prominent keel, venation originally with hyaline membrane, cross veins not discernible; estimated length of the mesothoracic wing pad about 9.4 mm, width approximately 5 mm; costal field of the mesothoracic wing pad broad and triangular; costal margin with prominent keel, first half of the anterior margin of the wing pad almost perpendicular to the body axis; faint vein CP in costal area bowed, running more or less parallel to ScP; concave ScP long and simple, weakly curved, running parallel to RA; RA and RP basally connected, RP separating from RA at about 1/3 of the wing-length from the base; convex RA long and simple, running to the apex

of the wing pad; concave RP distally forked into two branches reaching the posterior margin of the wing pad; stem of M and the point of divergence of MA and MP not discernible; convex MA simple, distally strongly curved; concave MP deeply forked with two branches; CuA and CuP basally fused, CuA diverging from CuP at about 1/4 of the wing-length from the base; convex CuA arched, divided into two main branches; concave CuP more or less parallel to CuA, deeply forked into two branches reaching the posterior margin of the wing pad; anal area with two simple anal veins preserved. Metathorax bearing wing pad with slender costal area and less obvious venation pattern; concave ScP simple, weakly curved, parallel to RA; RA and RP basally connected, RP diverging from RA at about a half of the wing-length; stem of M and the point of divergence of MA and MP not discernible; convex MA simple, concave MP probably forked into two branches; CuA and CuP basally fused, the point of divergence not preserved; convex CuA simple, concave CuP reaching the posterior margin of the wing pad with two terminal branches; anal area of the metathoracic wing pad disrupted, with only one anal vein weakly discernible.

Abdomen: Slowly tapering towards the rear with ten visible abdominal segments (estimated length of the second abdominal segment 2 mm); abdominal segment 1-4 partly covered by metathoracic wing pad; length of abdominal segments slowly decreasing towards the rear; all abdominal segments bearing pointed posterolaterally directed heart-shaped structures with a prominent groove in the middle, parallel to the anterior margin of the lobe; anterior margin of each lobe convex; last abdominal segment bearing a pair of cerci.

DISCUSSION

Morphotype B display the following combination of venation characters supporting its clear placement to the order Palaeodictyoptera: (1) wings in outstretched position protruding laterally, mesothoracic wing bearing prominent keel; (2) presence of broadly attached triangular prothoracic winglets; (3) presence of all main longitudinal veins distinctly corrugated.

Morphotype B has fore and hind wing similar in size and venation pattern although there are certain small differences. Fore wing is of nearly triangular shape due to prominent anterior keel indicating early immature instar. Meso- and metathoracic wing pads are broadly attached to their respective thoracic segments. All main longitudinal veins are present with prominent corrugation. The faint vein CP is recognizable in costal area remote from anterior margin of the wing pad (see Fig. 18F). ScP is simple, extending near the apex of the wing pad. RA and RP are basally connected, RP diverging from RA at about a half of the wing-length. RA is simple, whilst RP is divided into two branches. Stem of M is not discernible MA is simple, MP is probably deeply forked into two branches. CuA and CuP are basally fused, CuP diverging from CuA close to the base of the wing pad. CuA is arched, divided into two branches strongly curved to the posterior margin, CuP is forked with two branches.

The main difference between Morphotype B and Morphotype A is the presence of clearly branched vein CuA ending with two branches. Riek (1976) separated two superfamilies Homoiopteroidea and Spilapteroidea on the basis of branched CuA. Spilapteroidea bear also MA distinctly branched unlike in Morphotype B (Prokop & Nel, 2004).

For this reason we suppose the attribution of Morphotype B in Homoiopteroidea. This superfamily consists of two families as follows: Homoiopteridae Handlirsch, 1906 and Heolidae Handlirsch, 1906 (Sinitshenkova, 2002b).

In Homoiopteridae, the basal parts of ScP, RA, RP and M are gently arched (Sinitshenkova, 2002b; Carpenter, 1992). ScP is typically long, ending near the apex of the wing, RP has few branches, MA is simple and MP is branched. CuA

has usually several short branches, more or less parallel to CuP. Hind wings are broader than fore wings (Carpenter, 1992). These characters roughly corresponds with Morphotype B, and thus we propose to attribute the Morphotype B to the family Homoiopteridae.

Nevertheless, the association of Morphotype B with certain palaeodictyopterous family is very difficult because immature wings are not completely developed and venation pattern may not exactly correspond with the traits of adults. As it was mentioned above, during the development some other veinal branch can arise, thus originally two-branched vein can finally have five or more branches. Similarly, archedictyon present in selected palaeodictyopterous families can be developed later in ontogeny, thus it is not developed yet in the wings presented here (Sinitshenkova, 2002b; Prokop et al., 2012).

However, the reduction of branches is rather improbable and thus our delimitation mainly based on branched CuA evidenced for different placement of Morphotype A.

4. CONCLUSION

The material presented in this thesis consist of 14 specimens of Palaeodictyoptera immature stages preserved in sideritic iron nodules those were collected in Upper Carboniferous locality “Porąbka−Klimontów” near Sosnowiec (Silesia, Poland). It represents notable source of data on wing venation morphology and development as well as particularly variability of larvae of similar instars. Although palaeodictyopterids were abundant during the Late Paleozoic, the wings of their immature stages are poorly known due to lack of suitable fossils and also difficulties with systematic attribution.

For example, onisciform nymphs previously described as *Rochdalia parkeri* Woodward, 1913, and *Idoptilus onisciformis* Wootton, 1972 were due to lack of differentiating traits later removed from Palaeodictyoptera (Carpenter, 1992). Although the venation pattern in these nymphs is not well preserved, the overall habitus, presence of triangular prothoracic lobes and characteristic position of the wings with respect to their body strongly resembles Morphotype A and Morphotype B, thus we have no doubt about their palaeodictyopterous affinities.

The other described nymphs were attributed to the families Lycocercidae (*Lycodemas adolescens* Carpenter & Richardson, 1971) and Tchirkovaeidae (*Tchirkovaea guttata* Zalessky, 1931, *Tchirkovaea sharovi* Sinitshenkova, 1979 and *Paimbia fenestrata* Sinitshenkova, 1979).

We have followed the simplified key of Eupalaeodictyoptera established by Riek (1976) for attribution to certain superfamily, and system of Sinitshenkova (2002b) for possible association on familial level. Based on fore wing venation characters, we have distinguished two types of wings, for the purposes of this thesis termed as Morphotype A and Morphotype B. We have tentatively attributed the wings of Morphotype A to the family Breyeriidae because of the wing characters as follows: (1) precostal area present; (2) broad costal area of the wing; (3) anterior margin of the wing pad strongly curved; (4) MA and CuA unbranched; (5) MA not coalesced with RP; (6) CuA not braced with MP; (7) CuP with less than four branches; (8) MP, CuA and CuP strongly curved toward posterior margin of the

wing pad; (9) anal area of the hind wing more expanded. This attribution is also supported by the fact that members of the family Breyeriidae are already known from this period and equivalent site in the Czech part of the basin (see Kukalová, 1959), but familial attribution is not definite because of incompletely evolved venation pattern and morphological changes that may occur during the wing development (e.g., protraction and straightening of the wing).

A single specimen of Morphotype B we have distinguished from Morphotype A on the basis of having CuA distinctly two branched. Therefore, we have assigned Morphotype B to the family Homoiopteridae, which is according to Carpenter (1992) and Riek (1976) characterized by following characters: (1) MA unbranched; (2) CuA distinctly two branched.

Similarly as in Morphotype A, familial assignment is nevertheless problematic because the venation pattern of immature wings is not fully developed and does not provide a satisfactory concept of the adult wing venation pattern for comparison with the other known species of Palaeodictyoptera. Moreover, Morphotype B is represented by only a single specimen, thus broader comparison of specimens is unavailable like for the Morphotype A.

Finally, the results significantly contribute to the morphology of veinal variability and developmental traits of palaeodictyopteran larval wings. Certain structures like formation of costal area with vein CP remote from the wing margin was confirmed after Kukalová-Peck (1978).

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